RESUMEN.—Halcones Peregrinos (*Falco peregrinus*) jóvenes, que fueron sueltos en Milwaukee, Wisconsin en 1987, estuvieron activos y cazaron durante la noche. Desde el 8 al 16 de septiembre, encontramos 38 cuclillos de la especie *Coccyzus americanus,* 1 de la especie *C. erythropthalmus,* y 1 picogordo de la especie *Pheucticus ludovicianus,* que habían sido cazados en la noche; con un máximo de 13 aves el día 13 de septiembre. Muchas de las aves capturadas tenían los cuerpos abiertos y decapitados, lo que es consistente en las víctimas de Halcones Peregrinos.

[Traducción de Eudoxio Paredes-Ruiz]

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placed in the recently described genus *Ornichia* (KLACKENBERG, 1986). Three species were added during the 19th century. It was not until 1963 that the remaining taxa, *T. vohimavensis, T. platypterus* var. *angustialatus, T. pervillei, T. boivinii* and *T. antaisaka*, were described by HUMBERT in a preliminary paper when preparing the family *Gentianaceae* for the Flore de Madagascar et des Comores (not completed). All of the latter taxa are accepted in the present revision, but *T. platypterus* var. *angustialatus* is elevated to the rank of subspecies and *T. pervillei* and *T. boivinii*, not validly published by HUMBERT, are here validated. *T. umbellatus* is a new species described in the present paper.

Material has been examined from BM, K, MO, P and S (abbreviations according to HOLMGREN et al., 1981). Measurements in the descriptions are from dry material.

The spelling of geographical names is as much as possible in accordance with the Carte de Madagascar au 1 : 500000 Type 1963, Institut Géographique National, Paris, annexe Tananarive.

All drawings are by the author.

The taxa delimited in this work are in accordance with the discussion in KLACKENBERG (1985 : 9), i.e. in brief : 1) species are morphologically identifiable distinct populations ; 2) subspecies are two or several identifiable populations with intermediate forms in a contiguous area ; 3) varieties are locale deviating populations of a species ; 4) forms are deviating individuals. Varieties and forms are considered to be of no value in this work.

Tachiadenus is small and homogeneous and a division into sections of the genus is not thought necessary. Furthermore, to avoid paraphyletic groups *T. gracilis* would have to be the sole representative in its section, in any delimitation, which will be neither practical nor meaningful.

MORPHOLOGY

HABIT : The genus *Tachiadenus* consists of erect annual herbs with woody base to probably perennial subshrubs, from ca. 0.1 m (several species) to 3 m high (*T. tubiflorus*).

STEM : The stems are terete to subquadrangular. They are sometimes wingless (*T. tubiflorus*) but usually furnished with four wings or lines. The wings or lines are either situated at equal distance from each other or run more closely to each other in two pairs at opposite sides of the stem (*T. platypterus, T. longiflorus, T. pervillei* and *T. boivinii*). In *T. vohimavensis* the lines are also situated in two pairs at opposite sides of the stem, but below the attachments of the leaves, not between them, which is the usual state.

LEAVES : The leaves follow the usual pattern of the *Gentianaceae*. They are always decussate. The leaf pairs are usually separated by more or less elongated internodes, but when the inflorescence is umbel-shaped, two pairs of leaves might be very closely set just below the umbel (i.e. very short internode). The leaves are sometimes furnished with a distinct petiole (*T. longifolius* and *T. tubiflorus*). However, the petiole is usually indistinct or the leaves are sessile. Distinctly amplexicaul leaves are characteristic only to *T. antaisaka*, but semiamplexicaul leaves are found in *T. platypterus, T. longiflorus* and *T. pervillei*. The leaves are always simple and entire. The outline of the leaves is usually narrowly ellip-

tic to narrowly ovate but ovate and obovate leaves may be found. They are parallel-nerved with a prominent mid-nerve and 1-2 pairs of lateral nerves. The leaves are glabrous but small unicellular hair-like structures are present at the axils. The stomata are anisocytic.

INFLORESCENCE : The basic structure of the inflorescence is a di- to monochasial cyme. In five species, viz. *T. boivinii, T. antaisaka, T. umbellatus, T. longifolius* and *T. tubiflorus* the internodes of the inflorescence are shortened. In the latter four species this results in an almost total suppression of the internodes as well as the leaves (bracts) of the inflorescence, which manifests itself as an umbel-shaped inflorescence. This same evolution can also be observed within the Malagasy population of *Exacum* (KLACKENBERG, 1985 : 11).

CALYX : The calyx usually consists of five equal-sized and elongated valvate lobes coalescent 1/3-1/2 of their length and furnished with a wing at the dorsal side of each sepal. Some exceptions occur. *T. tubiflorus* has broad and overlapping calyx lobes of different size with two narrower outer and three broader inner ones forming a many-layered cornet. *T. gracilis* and *T. tubiflorus* have long free lobes and the sepals are coalescent only at the very base less than 1/5 of their length. In *T. platypterus* subsp. *platypterus* the sepals are coalescent 2/3-3/4 of their length with the free lobes turning outwards. These lobes are furthermore not subulate or linear but broadened in their middle part. *T. pervillei* is also furnished with broad sepal lobes though more elongated and less distinctly broadened at the middle than in *T. platypterus* subsp. *platypterus*. The dorsal wings in *T. vohimavensis, T. longiflorus* and *T. pervillei* are usually very distinct (up to 6 mm wide). On the contrary *T. boivinii* and *T. tubiflorus* lack wings completely. The wings of *T. carinatus* and *T. vohimavensis* are characteristic in being broad almost to the tip of the lobes and there rather abruptly narrowing. The calyx in *T. longiflorus* is unique in being furnished with 10 wings, i.e. except for the wings situated at each sepal along the mid-nerve, there are five more situated along the sutures between the sepals. These wings end at the lobe sinuses. The calyx of *T. antaisaka* is dotted with small epidermal papillae.

COROLLA : The flowers of *Tachiadenus* are pentamerous, showy, white to violet and large with a long narrow tube which varies from a few centimetres long in *T. gracilis* to up to 19 cm in some individuals of *T. boivinii*. Above the anthers all species, except *T. gracilis, T. antaisaka* and *T. umbellatus* and some individuals of *T. carinatus*, are furnished with a coronula within the tube. This coronula usually consists only of more or less prominent knobs immediately above the anthers or between the anthers and the mouth of the tube. In *T. longifolius* and *T. tubiflorus*, however, the coronula forms a coherent callus at the mouth. The latter species is also furnished with papillate hairs at the base of the petal lobes around the mouth of the tube.

The upper epidermis of the petals consists of conical more or less isodiametric cells covered with cuticular striations.

After anthesis the nerves in the petals harden and the corolla persists for a long time, but is eventually thrown off, usually torn apart just above the capsule. In *T. longifolius* and *T. tubiflorus* the corolla is also ultimately deciduous, but first the lower 1/4-1/3 of the tube distinctly harden and widens forming a hard tube around the young fruit. When the capsule matures the whole of this tube is rejected.

ANDROECIUM : The corolla tube, slightly widened where the stamens are contained below the limb, totally encloses the anthers. The anthers are inserted below the lobe sinuses on very short filaments. They are thin with soft walls. The endothecium walls consist of more or less parallel bars and the thecae open by longitudinal slits. This is in accordance with *Ornichia* and *Sebaea* but contrary to the hard anthers with finely perforated endothecium found in *Exacum* which open by apical pores (KLACKENBERG, 1985 : 15). The anthers are furnished with a small usually thin apical appendix. This appendix is truely apical as a continuation of the connective and not placed as a dorsal knob as in *Exacum*. In *T. tubiflorus* the appendix is broad with large papillae and in addition the same type of appendices are found at the bases of the thecae. Furthermore, the anthers are usually rectangular-linear standing together forming a tube, but the anthers of *T. tubiflorus* are broader at the base than at the apex and consequently form a cone.

GYNOECIUM : The ovary has parietal placentation but at least when young the placentas, which are long and running from top to base, stand together though not fused forming a partition. The ovary in this way appears to be bilocular. The placentas are covered with numerous ovules. The fruit is a bivalved capsule. The partition composed of the protruding mid-walls is in fruit partly to usually entirely coriaceous. In *T. tubiflorus* not only the mid-walls but also the involute placentas harden in fruit. The style is filiform and straight and at late anthesis usually protruding from the tube. The stigma is entire to faintly bilobed without any taxonomical value.

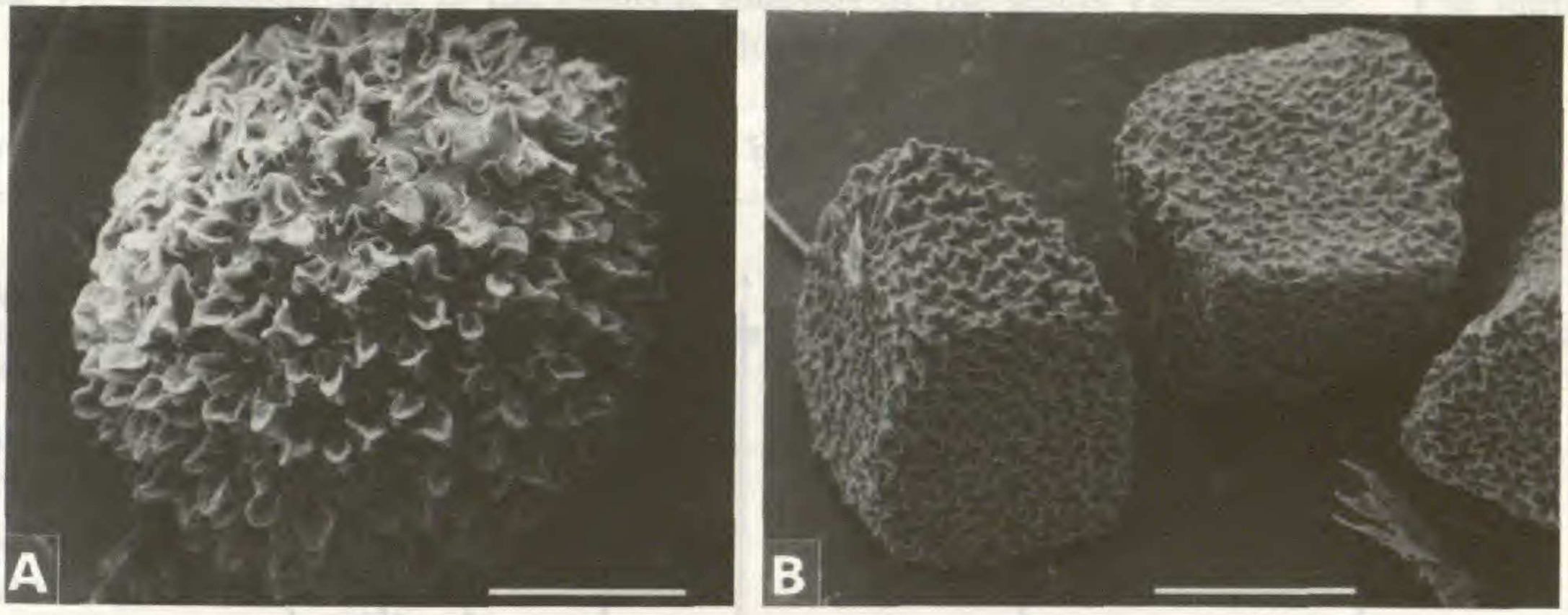
SEEDS : The seeds are numerous and small, 0.3-0.8 mm in diameter, usually angular and subconical with the testa cells anticlinally undulated in a star-shaped pattern (Pl. 1, *B*). This is the same seed morphology as is found in most of the genera within the *Exacinae*, e.g. *Ornichia, Exochaenium, Belmontia* and most of the species of *Exacum* (the primitive state within this genus). In *T. tubiflorus* the seeds are spherical, with the walls of the testa cells much protruding (Pl. 1, *A*). This type of seed has not been found in any other species of *Exacinae*.

No studies have been made on the karyology or the embryology of *Tachiadenus*.

PHYLOGENY

The phylogeny has been worked out by constructing a cladogram (Pl. 2) using HENNIG's (1966) argumentation method.

NODE A : The apomorphic characters within *Tachiadenus* have been identified using *Ornichia* as outgroup. *Tachiadenus* was placed in the subtribe *Tachiinae* by GILG (1895) but both *Tachiadenus* and *Ornichia* are probably better placed in the subtribe *Exacinae* (KLACKENBERG, 1985 : 17, 1986). Other possible taxa to use as outgroup in relation to *Tachiadenus* are *Exacum* and *Sebaea*, both in subtribe *Exacinae* (GILG, 1895) ; see KLACKENBERG (1985 : 19) for a further discussion. *Sebaea* is a somewhat polymorphic genus with unclear genus delimitation, often including *Exochaenium* and *Belmontia* (see MARAIS, 1961 : 464). *Ornichia, Tachiadenus* and *Exacum* are characterized by character (ch.) 25

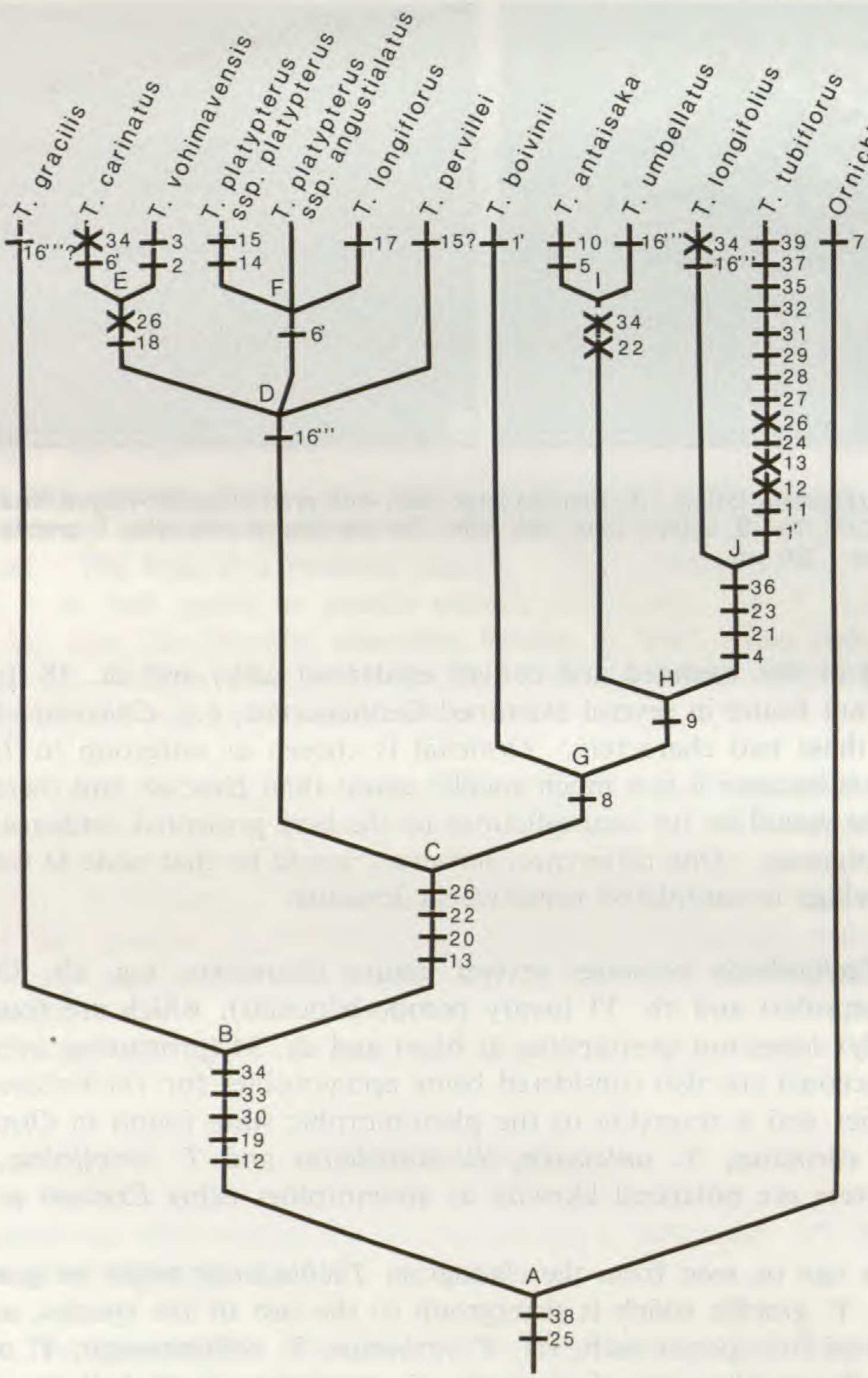


Pl. 1. — **Seeds of Tachiadenus** (SEM) : **A**, rounded large seeds with protruding star-shaped testa cells, *T. tubiflorus* (*s. coll.*, *SF-2378*, P) ; **B**, cubical seeds with rather flat star-shaped testa cells, *T. gracilis* (*J. & M. Peltier 4624*, P). — Scale : 200 μm.

(petals with more or less rounded and convex epidermal cells) and ch. 38 (testa cells star-shaped) which is not found in several examined *Gentianaceae*, e.g. *Chironia* which is chosen as outgroup for these two characters. *Ornichia* is chosen as outgroup to *Tachiadenus* in the present analysis because it is a much smaller genus than *Exacum* and therefore easier to work with. There would be no contradictions to the here presented cladogram when using *Exacum* as the outgroup. One difference, however, would be that node D would not exist, as having calyx wings is considered primitive in *Exacum*.

Node B : *Tachiadenus* possesses several unique characters, e.g. ch. 19 (long tube), ch. 30 (narrow capsules) and ch. 33 (ovary pseudo-bilocular), which are found in all species. Ch. 12 (calyx lobes not overlapping at base) and ch. 34 (protruding mid-walls in capsule entirely coriaceous) are also considered being apomorphies for *Tachiadenus* but are not found in all species and a reversion to the plesiomorphic state found in *Ornichia* must be postulated in *T. carinatus, T. antaisaka, T. umbellatus* and *T. longifolius*, respectively. These five characters are polarized likewise as apomorphies using *Exacum* as outgroup.

Node C : As can be seen from the cladogram *Tachiadenus* might be grouped in three main groups, i.e. *T. gracilis* which is sistergroup to the rest of the species, and two sistergroups comprised of five species each, viz. *T. carinatus, T. vohimavensis, T. platypterus, T. longiflorus* and *T. pervillei*, and *T. boivinii, T. antaisaka, T. umbellatus, T. longifolius* and *T. tubiflorus*, respectively. *T. gracilis* differs from the rest of the species by lacking all of the four characters ch. 13 (calyx lobes long coalescent), ch. 20 (tube more than twice the calyx length), ch. 22 (coronula present) and ch. 26 (large anthers). However, ch. 13 and ch. 26 are absent also in *T. tubiflorus* and ch. 22 is absent in *T. antaisaka* and *T. umbellatus* and reversals in these characters are proposed as the most parsimonious solution. There are also four specimens of *T. gracilis* at the far south of its distribution area



Pl. 2. — **Cladogram showing the phylogenetic relationship between the species of Tachiadenus.** The groupings, designated by a letter, are discussed in the text (see Phylogeny). The apomorphies are indicated with bars and numbers explained in Table 1. Crossed bars indicate a supposed reversal of an earlier acquired character. Apostrophes " ' " after a number indicate homoplastic characters with the number of the apostrophes equalling the number of supposed additional parallelisms occuring within *Tachiadenus*. A data matrix of the characters is presented in Table 2.

TABLE 1 : Characters used in the cladistic analysis of the genus *Tachiadenus*. The numbers correspond to the numbers in the cladogram (Pl. 2).

APOMORPHIC	PLESIOMORPHIC
STEM	STEM
1. Without lines or wings.	With lines or wings.
2. Lines situated close to each other in two opposite pairs decurrent below the attachment of the leaves.	Lines situated at equal distance from each other in two opposite pairs decurrent between the attachments of the leaves.
3. With many papillae at the nodes on the edging between the leaves (i.e. petiole bases).	Without or with few papillae and only inside the edging.
LEAVES	LEAVES
4. With long, distinct petiole.	Petiole ± short or leaves sessile.
5. Amplexicaul.	Not amplexicaul.
6. Obtuse.	Acute.
7. Hairy.	Glabrous.
INFLORESCENCE	INFLORESCENCE
8. Cymes with shortened internodes and the subtending leaves (bracts) to the flowers (at least the ones of the uppermost flowers) ± reduced.	Cymes with long internodes ; bracts of normal leaf-size.
9. Inflorescence umbel-shaped, i.e. cymes with very short internodes and bracts very small or scale-like.	Cymes with shortened or long internodes but not totally suppressed ; bracts of normal leaf-size or reduced but not totally suppressed.
CALYX	CALYX
10. Calyx with small epidermal papillae.	Epidermis of calyx smooth.
11. Lobes of different size.	Lobes of ± equal size.
12. Lobes not overlapping at the base.	Lobes overlapping at the base.
13. Lobes long coalescent, ca. 1/3 of their length or more.	Lobes short coalescent, ca. 1/5 of their length or less.
14. Lobes bent outwards.	Lobes straight.
15. Lobes with the outermost part distinctly dilated.	Lobes ± linear or gradually tapering from the base.
16. Lobes on the dorsal side with distinct wings > 1 mm.	Lobes flat or keeled to undistinctly winged.
17. Calyx with ten wings.	Calyx with five or no wings.
18. Wings ± abruptly tapering near the apex.	Wings gradually tapering.
COROLLA	COROLLA
19. Tube long.	Tube short.
20. Tube more than twice as long as the calyx.	Tube twice the calyx length or shorter.
21. Lower 1/3 of the tube hardened and broadened at late anthesis.	Lower part does not harden or broaden but sometimes with hardened veins only.
22. Coronula ± distinct, consisting of knobs or ring-shaped.	Without coronula.
23. Coronula ring-shaped, callus-like.	Coronula not callus-like.
24. With epidermal hairs at the base of the limb.	Without such hairs.
25. Petals with ± rounded and convex epidermal cells.	Petals with elongated flat cells.
ANDROECIUM	ANDROECIUM
26. Anthers large, > 5 mm long.	Anthers short, < 5 mm long.
27. Anthers forming a cone ; each anther broader at the base than at the apex.	Anthers forming a tube ; each anther as broad at the base as at the apex.
28. Anthers with large, large-celled apical appendix.	Apical appendix thin.
29. Thecae bases with appendices.	Thecae bases without appendices.

Apomorphic	Plesiomorphic
Gynoecium	**Gynoecium**
30. Capsule narrow, narrowly ovoid to narrowly ellipsoid.	Capsule broad, ellipsoid to usualy ovoid or broadly ovoid.
31. Each carpel of the capsule with several prominent veins.	Each carpel of the capsule with mid-nerve prominent only.
32. Surface of capsule rough.	Surface ± smooth.
33. Ovary pseudo-bilocular.	Ovary truly bilocular at least towards the base.
34. The two protruding mid-walls in capsule entirely coriaceous.	Mid-walls partially membranaceous.
35. Placenta in fruit hard and involute.	Placenta not hard.
Seeds	**Seeds**
36. Seeds large, > 0.6 × 0.6 mm.	Seeds small, < 0.6 × 0.6 mm.
37. Seeds spherical.	Seeds ± cubical.
38. Testa cells star-shaped.	Testa cells ± isodiametric.
39. Walls of testa cells much protruding.	Walls not much protruding.

with tubes slightly longer than twice the calyx length, which are, however, not taken into consideration here.

Node D, E, F : Six taxa are joined by the single ch. 16 (distinct calyx wing). This is a weak character which has arisen several times. In *Exacum* (Klackenberg, 1985) the same problems with this character with delimitation and parallelism are observed. Within *Tachiadenus* three parallelisms are supposed, viz. in *T. gracilis, T. umbellatus* and *T. longifolius*. The delimitation of what is a wing is of course somewhat arbitrary. As drawn here, i.e. distinct wing wider than 1 mm, some specimens of *T. longiflorus* fall outside the definition by having somewhat narrower wings, but they are always distinct. *T. gracilis* is usually furnished with a narrow keel only but a few specimens from southeast Madagascar have slightly wider wings exceeding 1 mm which is marked with a ? in the cladogram. The six taxa joined at node D are on general resemblance grouped in two groups, viz. *T. carinatus* and *T. vohimavensis*, and *T. platypterus, T. longiflorus* and *T. pervillei*, respectively. *T. vohimavensis* is obviously a small segregate of *T. carinatus* with which it is joined by the structure of the calyx wing (ch. 18, wing broad and rather abruptly narrowing at the apex). The other group is here presented with *T. pervillei* separate. This species, however, is united with *T. platypterus* subsp. *platypterus* by ch. 15 (broadened calyx lobes) and *T. pervillei* could be equally parsimoniously placed as sistergroup to *T. platypterus* subsp. *platypterus* and with a reversal in ch. 6 (obtuse leaves). Being indistinct, however, ch. 15 in *T. pervillei* is considered doubtful. I also prefer to avoid to present a cladogram showing a subspecies more closely related to another species than to the other subspecies of the same species. This is, however, also a possible solution though rarely accepted (see also Klackenberg, 1985, species concept, for an example in *Exacum*). However, the two subspecies of *T. platypterus, T. longiflorus* and *T. pervillei* are considered closely related.

TABLE 2 : Data matrix of the characters used in the cladistic analysis of the genus *Tachiadenus*. The numbers correspond to the characters described in Table 1. 0 = plesiomorphic state ; 1 = apomorphic state ; — = neither state (homology absent) ; ? = character indistinct.

		SPECIES												
		ORN	GRA	CAR	VOH	PLA	PLA	LFL	PER	BOI	ANT	UMB	LFO	TUB
						pla	ang							
C	1	0	0	0	0	0	0	0	0	0/1	0	0	0	1
H	2	0	0	0	1	0	0	0	0	0	0	0	0	—
A	3	0	0	0	1	0	0	0	0	0	0	0	0	0
R	4	0/1 *	0	0	0	0	0	0	0	0	0	0	1	1
A	5	0	0	0	0	0	0	0	0	0	1	0	0	0
C	6	0	0	0/1	0	1	0/1	0/1	0	0	0	0	0	0
T	7	1	0	0	0	0	0	0	0	0	0	0	0	0
E	8	0	0	0	0	0	0	0	0	1	1	1	1	1
R	9	0	0	0	0	0	0	0	0	0	1	1	1	1
	10	0/1 **	0	0	0	0	0	0	0	0	1	0	0	0
N	11	0	0	0	0	0	0	0	0	0	0	0	0	1
U	12	0	1	1	1	1	1	1	1	1	1	1	1	0
M	13	0	0	1	1	1	1	1	1	1	1	1	1	0
B	14	0	0	0	0	1	0	0	0	0	0	0	0	0
E	15	0	0	0	0	1	0	0	1?	0	0	0	0	0
R	16	0	0/1	1	1	1	1	1	1	0	0	1	1	0
	17	0	0	0	0	0	0	1	0	0	0	0	0	0
	18	0	0	1	1	0	0	0	0	0	0	0	0	—
	19	0	1	1	1	1	1	1	1	1	1	1	1	1
	20	0/1 *	0	1	1	1	1	1	1	1	1	1	1	1
	21	0	0	0	?	0	0	0	0	0	0	?	1	1
	22	0	0	0/1	1	1	1	1	1	1	0	0	1	1
	23	—	—	0	0	0	0	0	0	0	—	—	1	1
	24	0	0	0	0	0	0	0	0	0	0	0	0	1
	25	1	1	1	1	1	1	1	1	1	1	1	1	1
	26	0	0	0	0	1	1	1	1	1	1	1	0/1	0
	27	0	0	0	0	0	0	0	0	0	0	0	0	1
	28	0	0	0	0	0	0	0	0	0	0	0	0	1
	29	0	0	0	0	0	0	0	0	0	0	0	0	1
	30	0	1	1	1	1	1	1	1	1	1	1	1	1
	31	0	0	0	?	0	0	0	0	0	0	?	0	1
	32	0	0	0	?	0	0	0	0	0	0	?	0	1
	33	0	1	1	1	1	1	1	1	1	1	1	1	1
	34	0	1	0	?	1	1	1	1	1	0	0	0	1
	35	0	0	0	0	0	0	0	0	0	0	0	0	1
	36	0	0	0	?	0	0	0	0	0	0	?	1	1
	37	0	0	0	?	0	0	0	0	0	0	?	0	1
	38	1	1	1	1	1	1	1	1	1	1	1	1	1
	39	0	0	0	?	0	0	0	0	0	0	?	0	1

* *Ornichia trinervis* has distinct petioles and long corolla tube.

** Usually the calyx is devoid of papillae but in some specimens the calyx is sparsely furnished with longer papillae/hairs.

NODE G, H : The third group comprising *T. boivinii, T. antaisaka, T. umbellatus, T. longifolius* and *T. tubiflorus* is characterized by a transformation of the inflorescence, first at node G with ch. 8 (shortened internodes in the inflorescence) and also at node H by ch. 9 (inflorescence umbel-shaped). This transformation of cymes is also observed in the Malagasy and Socotrian species of *Exacum* but not within their Asian population (KLACKENBERG, 1985). Though this character is supposed to have arisen several times within *Exacum* the most parsimonious solution in *Tachiadenus* is to propose one single transformation in that direction.

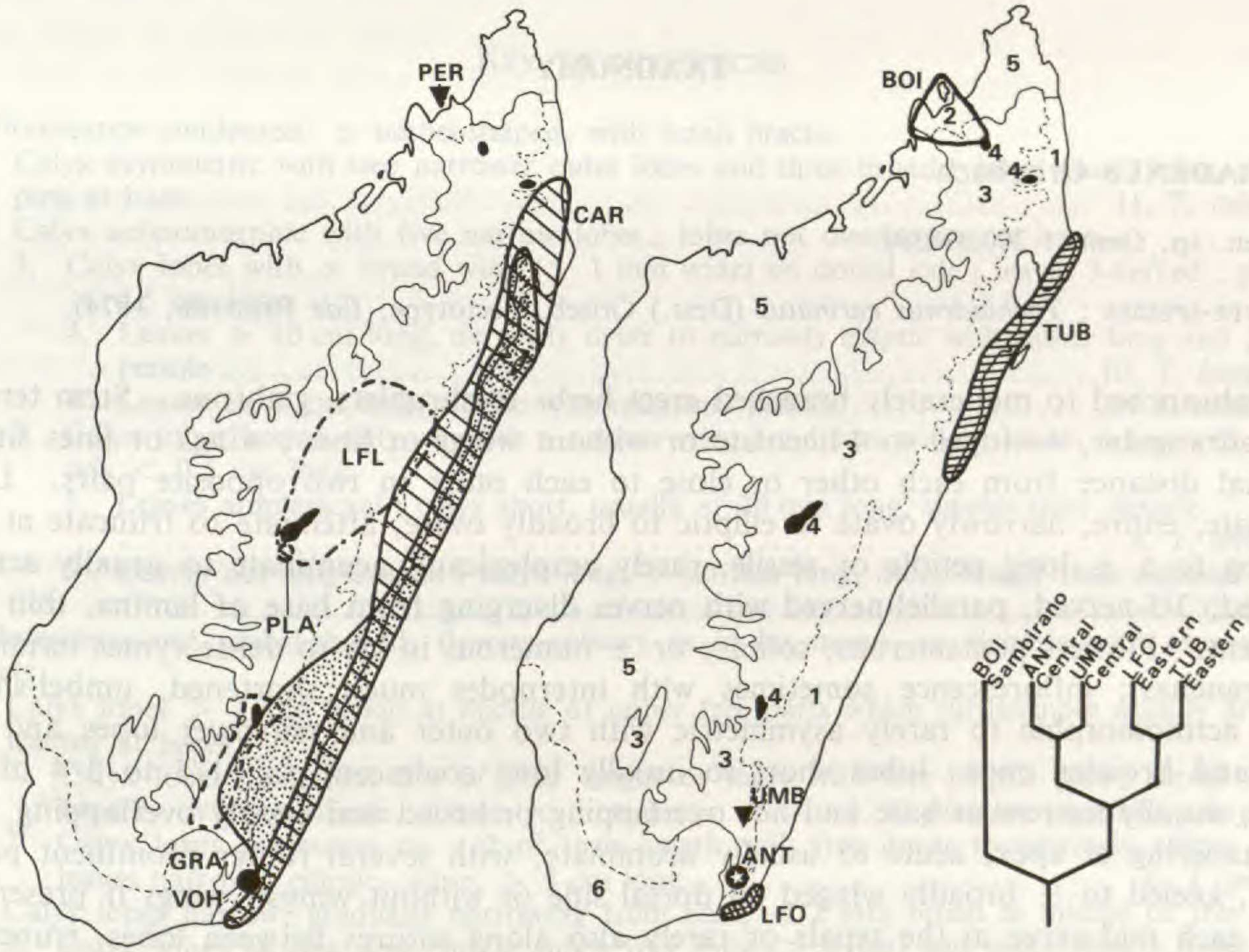
NODE I : The species pairs *T. antaisaka* and *T. umbellatus*, and *T. longifolius* and *T. tubiflorus* are well corroborated. The two local endemics *T. antaisaka* and *T. umbellatus* are united by two reversals, in ch. 22 (coronula present), found also only in the distantly related *T. gracilis*, and ch. 34 (septa entirely coriaceous) found also in *T. gracilis* and *T. carinatus*.

NODE J : *T. longifolius* and *T. tubiflorus* form a well corroborated group united by four unique characters, viz. ch. 4 (long petiole), ch. 21 (lower part of corolla hardening in fruit), ch. 23 (coronula ring-formed) and ch. 36 (large seeds). The reversal of ch. 26 (long anthers) in *T. tubiflorus* might also be placed at node J as short anthers sometimes occur in *T. longifolius* as well. It is interesting to note the many autapomorphies attributed to *T. tubiflorus*. According to the characters observed, *T. tubiflorus* has undergone 24 evolutionary steps, compared to the single (doubtful) one for *T. gracilis*.

PHYTOGEOGRAPHY (Pl. 3)

Tachiadenus is endemic to Madagascar where it is distributed along the eastern coast and the central mountain chain from sea-level up to almost 2000 m. It is also found in the northern part of the west coast in the island of Nossi Be and the adjoining part of the main island. This corresponds with the East Malagasy Region of WHITE (1983) based on HUMBERT (1955). The species are usually restricted to only one each of the phytogeographical Domains presented in WHITE (1983). They are absent from the Domain of the High Mountains, but present in the other three. *T. longifolius* and *T. tubiflorus* are found in the southern and northern parts of the Eastern Domain, respectively. *T. pervillei* is restricted to the island of Nossi Be in the Sambirano Domain and *T. longiflorus, T. platypterus, T. antaisaka, T. umbellatus* and *T. vohimavensis* are all found only in the elevated Central Domain. *T. boivinii* is mainly found in the Sambirano Domain but also in the adjoining part of the more elevated Central Domain in Tsaratanana. Finally, the two widely spread and sympatric *T. gracilis* and *T. carinatus* are distributed in almost the whole of the Eastern Domain, but reach also the more elevated (> 800 m altitude) contiguous parts of the Central Domain.

A brief comment on the cladogram (Pl. 2 and 3) with reference to vicariance biogeography may be of interest. The north-south vicariance along the shore within the Eastern Domain between *T. longifolius* and *T. tubiflorus* is distinct and well corroborated. The likewise north-south vicariance in the southern mountain chain between *T. antaisaka* and *T.*



Pl. 3. — **Phytogeography** : The generalized distribution of the species of *Tachiadenus* compared with the phytogeographical regions of HUMBERT (1955), recently also presented by WHITE (1983). The regions are : East Malagasy Region : 1, Eastern Domain ; 2, Sambirano Domain ; 3, Central Domain ; 4, Domain of the high Mountains. West Malagasy Region : 5, Western Domain ; 6, Southern Domain. The species are abbreviated with the three first letters of their epithets except for LFL = *T. longiflorus* and LFO = *T. longifolius*. For the five species presented at the right-hand map, a cladogram showing the vicariance between the domains based on *Tachiadenus* is given.

umbellatus (Central Domain) is also obvious. It is further interesting to note that these two species pairs, belonging to the Eastern and Central Domains, respectively, vicariate between themselves. Furthermore, together they vicariate with the north-eastern *T. boivinii* mainly from the Sambirano Domain. Thus, according to this only cladogram and therefore of course highly uncertain, Eastern and Central Domains should be more closely related to each other than any of them is to the Sambirano Domain. The group united at node D is too uncertain to render any comments. It may also be noted that the most primitive species, *T. gracilis*, is also the most widespread one.

TAXONOMY

TACHIADENUS Grisebach

Gen. sp. Gent. : 200 (1839).

TYPE-SPECIES : *Tachiadenus carinatus* (Desr.) Griseb. (lectotype, *fide* PFEIFFER, 1874).

Unbranched to moderately branched erect herbs to shrublets, glabrous. Stem terete to subquadrangular, 4-winged to 4-lineolate or without wings or lines ; wings or lines situated at equal distance from each other or close to each other in two opposite pairs. Leaves decussate, entire, narrowly ovate to elliptic to broadly ovate, attenuate to truncate at base, tapering to a ± long petiole or sessile, rarely amplexicaul, acuminate to usually acute to rounded, 3-5-nerved, parallel-nerved with nerves diverging from base of lamina, thin to ± succulent. Flowers pentamerous, solitary or ± numerous in lax to dense cymes terminal at the branches ; inflorescence sometimes with internodes much shortened, umbel-shaped. Calyx actinomorphic to rarely asymmetric with two outer and narrower lobes and three inner and broader ones ; lobes short to usually long coalescent, ca. 1/5 to 3/4 of their lenght, usually narrow at base and not overlapping or broad and clearly overlapping, gradually tapering at apex, acute to usually acuminate, with several rather prominent parallel nerves, keeled to ± broadly winged on dorsal side or without wings ; wings if present one along each mid-nerve at the sepals or rarely also along sutures between lobes, truncate to usually tapering at base, somewhat abruptly to usually gradually tapering at apex, sometimes accrescent (?) in fruit, without prominent veins. Corolla actinomorphic, contorted in aestivation with petals basally connate forming a long to very long tube, usually large, eventually decidious after anthesis, rarely widening and hardening at lower part of tube at late anthesis, with or without a coronula of small knobs above anthers or as a ring-formed callus at mouth of tube, white or blue to violet ; lobes spreading (?), elliptic to broadly ovate to almost rounded, obtuse to acuminate. Stamens inserted in tube at a distance below the sinuses ; filaments very short, much shorter than anthers, free ; anthers not exserted and ± cohering to each other in a ring, ± rectangular to somewhat conical, deeply cleft at base, usually with a thin appendix at apex but rarely with larger and large-celled appendices at apex and at thecae bases, straight, dehiscing by slits to base. Pollen grains isopolar, radially symmetrical, 3-colporate, spheroidal to prolate, medium-sized with polar axis 27-45 μm and equatorial diameter 22-25 μm ; exine ± smooth with slits or conical depressions, with perforations. Ovary pseudo-bilocular due to parietal placentas protruding to centre ; ovules many. Style filiform, long, straight. Stigma entire to faintly bilobed. Fruit a capsule, narrowly ovoid to narrowly ellipsoid, gradually attenuate at apex, coriaceous and septicidally 2-valved ; protruding mid-walls usually entirely coriaceous to sometimes partially membranaceous. Seeds numerous, minute, angular to rarely rounded ; testa cells with star-shaped walls.

Genus of 11 species endemic to Madagascar found in the whole of the eastern region.

Key to the species

1. Inflorescence condensed, ± umbel-shaped, with small bracts.
   2. Calyx asymmetric with two narrower outer lobes and three broader inner ones ; lobes overlapping at base ..... 11. *T. tubiflorus*
   2′. Calyx actinomorphic with five narrow lobes ; lobes not overlapping at base.
      3. Calyx lobes with ± broad wing (> 1 mm wide) on dorsal side ; leaves 3-nerved ; pedicels > 0.5 cm long.
         4. Leaves > 10 cm long, narrowly ovate to narrowly elliptic with rather long and distinct petiole ..... 10. *T. longifolius*
         4′. Leaves ca. 5 cm long, elliptic with indistinct petiole ..... 9. *T. umbellatus*
      3′. Calyx lobes keeled only, or with a narrow wing (< 1 mm wide) ; leaves 3-5-nerved ; pedicels < 0.5 cm long.
         5. Leaves amplexicaul ; calyx short, usually < 20 mm long, shorter than capsule ..... 8. *T. antaisaka*
         5′. Leaves not amplexicaul ; calyx long, > 20 mm long, much longer than capsule ..... 7. *T. boivinii*
1′. Inflorescence not umbel-shaped, flowers solitary or in lax mono- or dichasia with normal-sized bracts.
   6. Calyx lobes > 2 mm broad at middle of upper free parts which furthermore usually are contracted at bases.
      7. Calyx lobes coalescent 2/3 of their length or more with free elliptic part ; leaves usually broadly ovate to elliptic, obtuse, < 5 cm long ..... 4. *T. platypterus* subsp. *platypterus*
      7′. Calyx lobes coalescent ca. 1/2 of their length with free linear to narrowly elliptic part ; leaves narrowly elliptic, acute, > 5 cm long ..... 6. *T. pervillei*
   6′. Calyx lobes narrow, gradually narrowing from base, < 2 mm broad at middle of free parts.
      8. Calyx wings lacking and corolla tubes very long (> 6 cm) and more than 3 times calyx length ..... 7. *T. boivinii*
      8′. Calyx wings present or absent ; if absent then corolla tube short (< 6 cm ; < 3 times calyx length).
         9. Leaves semiamplexicaul, sessile with leaf bases of opposite leaves almost adjoining and decurrent near each other between leaves.
            10. Calyx with additional wings along sutures between sepals, i.e. calyx 10-winged. ..... 5. *T. longiflorus*
            10′. Calyx keeled or winged along mid-nerve of lobes only, i.e. 5-winged ..... 4. *T. platypterus* subsp. *angustialatus*
         9′. Leaves not semiamplexicaul nor amplexicaul, usually ± petiolate with leaf bases decurrent at equal distance from each other or in two opposite pairs decurrent below respective leaves.
            11. Calyx keeled only or with narrow wing usually <1 mm wide ; corolla tube at most ca. twice as long as calyx ..... 1. *T. gracilis*
            11′. Calyx distinctly winged ; corolla tube more than twice as long as calyx.
               12. Leaves narrowly ovate, acuminate ; corolla white ..... 3. *T. vohimavensis*
               12′. Leaves usually ± elliptic, acute to obtuse ; corolla blue to violet ..... 2. *T. carinatus*

1. **Tachiadenus gracilis** Griseb. — Pl. 4 ; 15, *A* (map)

In DC., Prodr. 9 : 82 (1845).

Lectotype (here selected) : *Bojer s.n.*, Hab. in pratis humidis ad margines sylvarum ins. Madagascar, 1830 (W).

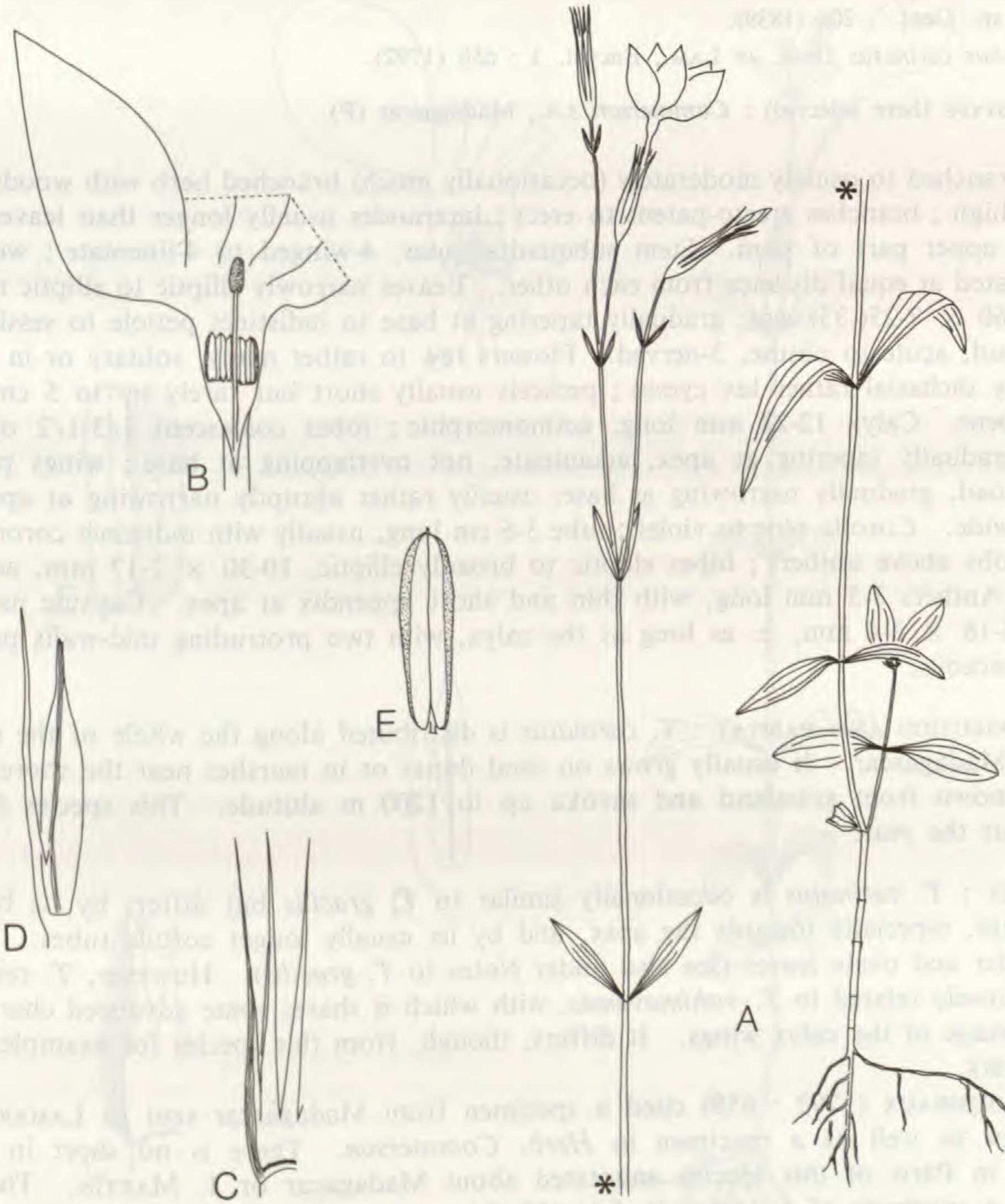
Unbranched to moderately branched herb with woody base, 0.2-1.1 m high ; branches ± erect ; internodes usually longer to much longer than leaves, especially at upper part of stem. Stem subquadrangular, 4-lineolate ; lines situated at equal distance from each other. Leaves very narrowly elliptic to narrowly ovate, 25-70 × 3-15 mm, gradually tapering at base to indistinct petiole to subsessile, not amplexicaul, acute to acuminate, 3-nerved. Flowers rather few, solitary or in mono- or usually dichasial lax cymes ; pedicels long, usually between 2-7 cm, usually slightly bent just below flower. Calyx 15-35 mm long, actinomorphic ; lobes coalescent ca. 1/5 of their length or less, subulate, not overlapping at base ; wings usually absent but sometimes with keel or narrow wing < 1(-2) mm wide. Corolla blue to violet ; tube 20-35(-45) mm long, without coronula ; lobes ovate to elliptic, 15-25 × 7-15 mm, acute. Anthers 2.5-4 mm long, with thin and short appendix at apex. Capsule narrowly ovoid to narrowly ellipsoid, 12-18 × 2-4 mm, shorter than calyx, with the two protruding mid-walls entirely coriaceous.

DISTRIBUTION AND HABITAT : *T. gracilis* is distributed along the eastern coast of Madagascar usually not far from the shore. It is found from sea level up to 1300 m altitude in forest or grassland on sand or in marshes. Flowering specimens seen from March to December.

NOTES : This species is characterized by its narrow leaves and usually sparsely branched habit, as well as the short corolla tubes (ca. twice the calyx length). There are a few specimens, however, which have slightly longer tubes (three specimens from the southern locality Fort-Dauphin area and one from unknown locality). These specimens have also other traits of *T. carinatus*, e.g. shorter pedicels, narrowly winged calyx and calyx lobes coalescent slightly longer than is usual. The calyx wings, however, are always gradually tapering towards the apex. In the north, *T. gracilis* has broader leaves and is less " gracile ", becoming somewhat similar in habit to *T. carinatus*.

SPECIMENS EXAMINED. — TAMATAVE : Ambila (— Lemaitso), 1951, *Benoist 809* (P) ; Sainte-Marie, 1850, *Boivin s.n.* (P) ; Ilaka, 1962, *Bosser 17001* (MO, P) ; Tamatave, 1954, *Bosser & Descoings 185* (MO) ; Pointe à Larrée, *Catat 2528* (P) ; Env. de Maroantsetra, 1912, *Perrier 9039* (P, S) ; Sainte-Marie et Angontsi, *Richard 15* (P). — TULEAR : Manantenina, 1925, *Decary 3867* (P) ; Fort-Dauphin, 1932, *Decary 10015* (P) ; Just east of Mandrondromotra, about 20 km north of Fort-Dauphin, 30 m, 1970, *Fosberg 52572* (MO) ; Env. de Fort-Dauphin près de Nahampohana (Nampoana), 1-25 m, *Humbert 5755* (P) ; Env. de Fort-Dauphin, forêt de Mandena, 1960, *Keraudren 1049* (P) ; Env. de Fort-Dauphin, 1970, *Keraudren-Aymonin & Aymonin 24980, 25021* (P) ; Env. de Fort-Dauphin, 1897, *Paroisse 49* (P) ; Distr. de Fort-Dauphin, Mandronodromotra, 1959, *Peltier 1507* (P). — FIANARANTSOA : Env. d'Ivohibe, ca. 1200 m, 1924, *Armand 12* (P) ; Forêt à l'ouest de Vondrozo, 1963, *Bosser 18632* (P, S) ; Prov. de Farafangana, Midongy du Sud, 1926, *Decary 5012* (K, P) ; Forêt à l'est d'Ivohibe, ca. 1000 m, 1924, *Humbert 3173* (K, P, S) ; Haute vallée de l'Iatara, bassin du Manampatra, 500-800 m, *Humbert 3406* (P) ; Entre le col du Kalambatitra et la vallée de la Manambolo, affluent de l'Ianaivo (Ionaivo), 1300 m, 1933, *Humbert 12098* (P, S) ; Distr. Ivohibe, Cant. Ivongo, 1961, *Razafindrakoto 11580 RN* (P) ; Farafangana, *Inst. Malg. de Recherche appl. 2095* (P).

INEXACT OR UNIDENTIFIED LOCALITIES : North Madagascar, *Baron 6093* (BM, K, P) ; Madagascar, *Bernard 1903* (P) ; Madagascar, *Bojer s.n.* (P) ; Prov. de Mananjary, 1909, *Geay 7203* (P) ; Madagascar, 1881, *Lantz 20* (P) ; Entre le Matitana(na) et le Mananjary, 1911, *Perrier 9071* (P) ; Bassin du Manampatra(na), haute vallée du T(S)ankara, 700 m, 1919, *Perrier 12597* (P) ; Madagascar, *Richard 98* (P) ; Près de la forêt de Marovetsetra, Ivohibe-Bara, 1924, *Herb. d'Alleizette 12* (P) ; Mauritius or Madagascar, *Herb. Brown & Hooker s.n.* (K) ; s. loc., *Herb. du Petit-Thouars* (P).



Pl. 4. — **Tachiadenus gracilis** : **A**, habit × 0.5 ; **B**, dissected upper part of flower × 1.5 ; **C**, part of calyx × 1.5 ; **D**, flower in fruit with corolla and most of calyx removed × 1.5 ; **E**, anther × 6. (A, *Humbert 12098*, S ; B, C, E, *Perrier de la Bâthie 12597*, P ; D, *Bosser 18632*, S).

2. **Tachiadenus carinatus** (Desr.) Griseb. — Pl. 5 ; 15, *B* (map).

Gen. sp. Gent. : 200 (1839).

— *Lisianthus carinatus* Desr. *in* Lam., Encycl. 3 : 658 (1792).

Lectotype (here selected) : *Commerson s.n.*, Madagascar (P).

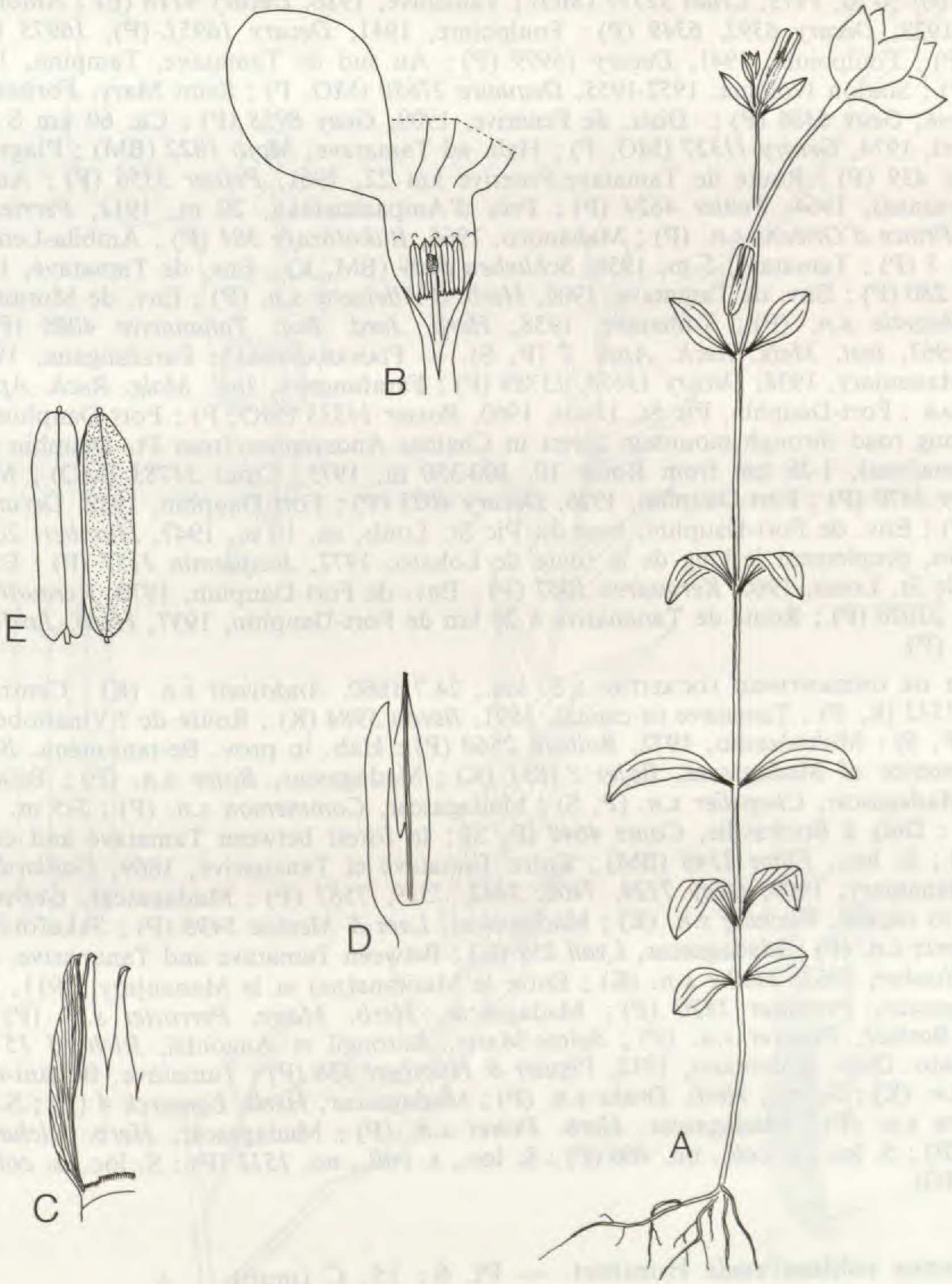
Unbranched to usually moderately (occasionally much) branched herb with woody base, 0.1-1 m high ; branches erecto-patent to erect ; internodes usually longer than leaves especially in upper part of stem. Stem subquadrangular, 4-winged to 4-lineolate ; wings or lines situated at equal distance from each other. Leaves narrowly elliptic to elliptic to obovate, 20-60 × 7-25(-35) mm, gradually tapering at base to indistinct petiole to sessile, not amplexicaul, acute to obtuse, 3-nerved. Flowers few to rather many, solitary or in mono- or usually dichasial rather lax cymes ; pedicels usually short but rarely up to 5 cm long, usually bent. Calyx 12-22 mm long, actinomorphic ; lobes coalescent 1/3-1/2 of their length, gradually tapering at apex, acuminate, not overlapping at base ; wings present, rather broad, gradually narrowing at base, usually rather abruptly narrowing at apex, ca. 1-3 mm wide. Corolla blue to violet ; tube 3-6 cm long, usually with indistinct coronula of small knobs above anthers ; lobes elliptic to broadly elliptic, 10-30 × 7-17 mm, acute to obtuse. Anthers 3-5 mm long, with thin and short appendix at apex. Capsule narrowly ovate, 13-18 × 3-4 mm, ± as long as the calyx, with two protruding mid-walls partially membranaceous.

Distribution and habitat : *T. carinatus* is distributed along the whole of the eastern coast of Madagascar. It usually grows on sand dunes or in marshes near the shore but it is also known from grassland and savoka up to 1200 m altitude. This species flowers throughout the year.

Notes : *T. carinatus* is occasionally similar to *T. gracilis* but differs by its broader calyx wings, especially towards the apex, and by its usually longer corolla tubes. It also has broader and ovate leaves (see also under Notes to *T. gracilis*). However, *T. carinatus* is more closely related to *T. vohimavensis*, with which it shares some advanced characters, e.g. the shape of the calyx wings. It differs, though, from this species for example by its blue flowers.

Desrousseaux (1792 : 659) cited a specimen from Madagascar sent to Lamarck by J. Martin as well as a specimen in *Herb. Commerson*. There is no sheet in *Herb. Lamarck* in Paris of this species annotated about Madagacar or J. Martin. There is, however, a specimen of Commerson from Madagascar in the general herbarium, which I have chosen as lectotype.

Specimens examined. — Diego-Suarez : Madagascar, Nosy Ngontsy (Angontsi), 1847-1852, *Boivin s.n.* (P) ; Distr. Andapa, Cant. Doany, 1956, *Christophe 8287 RN* (P) ; Env. de Sambava, massif d'Ambatobiribiry, 50-345 m, 1950, *Humbert & Capuron 24447* (P, S) ; P.K. 15, route Sambava-Vohemar, 1967, *Morat 2806* (P). — Tamatave : Tamatave, 29.7.1912, *Afzelius s.n.* (K, S) ; R.N. 5, ca. 5 km S of Foulpointe, 1984, *Barnett & Dorr 252* (MO) ; Env. d'Ambila (— Lemaitso), 1951, *Benoist 775* (P) ; Entre Brickaville et Ambila, 1966, *Boiteau 477* (P, S) ; Sainte-Marie, 1849, *Boivin 1792* (P) ; Foulpoint, *Bojer s.n.* (P) ; Along Route 2 from 45 km S of Tamatave to Tamatave, < 50 m,



Pl. 5. — **Tachiadenus carinatus** : **A**, habit × 0.5 ; **B**, dissected upper part of flower × 1.5 ; **C**, part of calyx × 1.5 ; **D**, flower in fruit with corolla and most of calyx removed × 1.5 ; **E**, anther × 6. (**A**, *Humbert 20396*, S ; B, C, E, *Humbert & Capuron 24447*, S ; D, *Chapelier s.n.*, S).

1975, *Croat 32441* (MO) ; Along Route 5 between Tamatave and Fenerive at PK 45, sea level, 1975, *Croat 32480* (MO) ; *id.*, PK 61 near S edge of Onibe River, > 50 m, 1975, *Croat 32522* (MO) ; *id.*, PK 80-PK 100, 50 m, 1975, *Croat 32577* (MO) ; Tamatave, 1926, *Decary 4118* (P) ; Ambila au sud de Tamatave, 1928, *Decary 6392, 6349* (P) ; Foulpointe, 1941, *Decary 16951* (P), *16973* (BM, P, S), *17008* (K, P) ; Foulpointe, 1941, *Decary 16999* (P) ; Au sud de Tamatave, Tampina, 1942, *Decary 17709* (K, P) ; Station Ivoloina, 1952-1955, *Dequaire 27630* (MO, P) ; Saint Mary, *Forbes s.n.* (K) ; S de Soanierana, *Geay 6386* (P) ; Distr. de Fenerive, 1909, *Geay 8958* (P) ; Ca. 60 km S of Fenerive, near sea level, 1974, *Gentry 11327* (MO, P) ; Hab. ad Tamatave, *Majo 1822* (BM) ; Plage Foulpointe, 1964, *Morat 439* (P) ; Route de Tamatave-Fenerive km 22, 1961, *Peltier 3356* (P) ; Antetezambaro (-Marotandrazana), 1964, *Peltier 4624* (P) ; Près d'Ampasimeloka, 20 m, 1911, *Perrier 7478* (P) ; Mahambo, *Prince d'Orléans s.n.* (P) ; Mahanoro, 1966, *Rakotozafy 581* (P) ; Ambila-Lemaitso, 1967, *Rosemolson 7* (P) ; Tamatave, 5 m, 1959, *Schlieben 8009* (BM, K) ; Env. de Tamatave, 1912, *Viguier & Humbert 280* (P) ; Env. de Tamatave, 1906, *Herb. d'Alleizette s.n.* (P) ; Env. de Moramanga, 1906, *Herb. d'Alleizette s.n.* (P) ; Tamatave, 1938, *Herb. Jard. Bot. Tananarive 4086* (P) ; Ambila-Lemaitso, 1967, *Inst. Malg. Rech. Appl. 7* (P, S). — FIANARANTSOA : Farafangana, 1970, *Boiteau 2094* (P) ; Mananjary, 1938, *Decary 13676, 13789* (P) ; Farafangana, *Inst. Malg. Rech. Appl. 2094* (P, S). — TULEAR : Fort-Dauphin, Pic St. Louis, 1960, *Bosser 14333* (MO, P) ; Fort-Dauphin, *Cloisel 64, 88* (P) ; Along road through mountain forest in Chaines Anosyennes from Ft. Dauphin to Ranomafana (Ranamafona), 1-28 km from Route 10, 100-350 m, 1975, *Croat 31783* (MO) ; Manantenina, 1925, *Decary 3870* (P) ; Fort-Dauphin, 1926, *Decary 4025* (P) ; Fort-Dauphin, 1932, *Decary 9788* (P) ; *id., 9844* (P) ; Env. de Fort-Dauphin, base du Pic St. Louis, ca. 10 m, 1947, *Humbert 20396* (P, S) ; Fort-Dauphin, peuplement le long de la route de Lokaro, 1972, *Jacquemin 1157* (P) ; Env. de Fort-Dauphin, Pic St. Louis, 1960, *Keraudren 1067* (P) ; Env. de Fort-Dauphin, 1970, *Keraudren-Aymonin & Aymonin 25020* (P) ; Route de Tananarive à 20 km de Fort-Dauphin, 1937, *Herb. Jard. Bot. Tananarive 2634* (P).

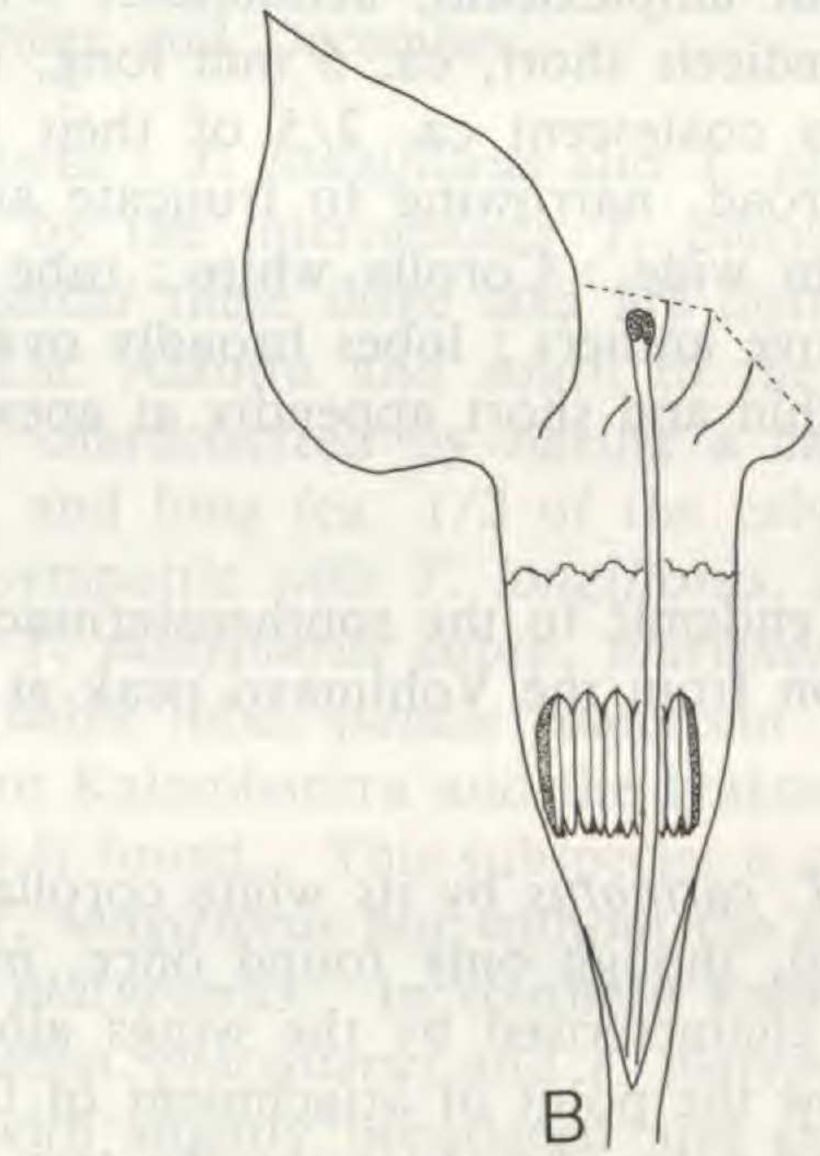
INEXACT OR UNIDENTIFIED LOCALITIES : S. loc., 24.7.1860, *Andovant s.n.* (K) ; Central Madagascar, *Baron 1512* (K, P) ; Tamatave to capital, 1891, *Baron 5984* (K) ; Route de ? Vinanobe, 1972, *Boiteau 2516* (P, S) ; Mohialamho, 1972, *Boiteau 2560* (P) ; Hab. in prov. Be-tani-mena, *Bojer (Boyer) s.n.* (K) ; Interior of Madagascar, *Bojer ? 1857* (K) ; Madagascar, *Bojer s.n.* (P) ; Belavena, *Catat 4328* (P) ; Madagascar, *Chapelier s.n.* (P, S) ; Madagascar, *Commerson s.n.* (P) ; 3-5 m, 1946, *Cours 2935* (P, S) ; Didy à Brickaville, *Cours 4648* (P, S) ; In forest between Tamatave and capital, *Elliot 1782* (K, P) ; S. loc., *Elliot 2146* (BM) ; Entre Tamatave et Tananarive, 1869, *Gaillardot 115* (P) ; Prov. de Mananjary, 1909, *Geay 7124, 7406, 7442, 7519, 7587* (P) ; Madagascar, *Gerrard 128, s.n.* (K) ; Coast to capital, *Kitching s.n.* (K) ; Madagascar, *Lam & Meeuse 5498* (P) ; Sakafotsy, 1000-1200 m, 1881, *Lantz s.n.* (P) ; Madagascar, *Lyall 259* (K) ; Between Tamatave and Tananarive, *Herb. Commerson & Hooker*, 1862, *Meller s.n.* (K) ; Entre le Matitana(na) et le Mananjary, 1911, *Perrier 9071* (P) ; Madagascar, *Perrottet 1820* (P) ; Madagascar, *Herb. Maire, Perrottet s.n.* (P) ; Madagascar, *Herb. Barbier, Pourret s.n.* (P) ; Sainte-Marie, Antongil et Angontsi, *Richard 15* (P) ; Prov. d'Andovoranto, Distr. Anivorano, 1912, *Viguier & Humbert 458* (P) ; Tamatave, Be-tani-mena, *Herb. Blackburn s.n.* (K) ; S. loc., *Herb. Drake s.n.* (P) ; Madagascar, *Herb. Lamarck 4* (P) ; S. loc., *Herb. Petit-Thouars s.n.* (P) ; Madagascar, *Herb. Poiret s.n.* (P) ; Madagascar, *Herb. Richard & Herb. Drake s.n.* (P) ; S. loc., *s. coll.*, no. *400* (P) ; S. loc., *s. coll.*, no. *1512* (P) ; S. loc., *s. coll. (? Cours)*, no. *2935* (MO).

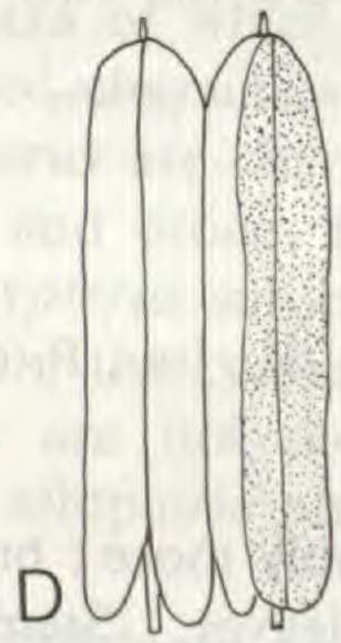
3. **Tachiadenus vohimavensis** Humbert. — Pl. 6 ; 15, *C* (map).

Adansonia, ser. 2, 3 (3) : 349 (1963).

TYPE : *Humbert 20719*, Tulear, Bassin de la Manampanihy, mont Vohimavo au nord d'Ampasimena, alt. 830 m, March 1947 (holo-, P) ; only known material.

Moderately branched shrublet, ca. 0.5 m high ; branches ± erect ; internodes varying in length but usually shorter than leaves. Stem subquadrangular, 4-winged ; wings situated





Pl. 6. — **Tachiadenus vohimavensis** : **A**, habit × 0.5 ; **B**, dissected upper part of flower × 1.5 ; **C**, part of calyx × 1.5 ; **D**, anther × 6. (A-D, *Humbert 20719*, P).

close to each other in two opposite pairs. Leaves narrowly ovate, 35-50 × 10-13 mm, rather abruptly tapering at base to short petiole, not amplexicaul, acuminate, 3-nerved. Flowers few, usually solitary at ends of branches ; pedicels short, ca. 5 mm long, usually bent. Calyx ca. 25 mm long, actinomorphic ; lobes coalescent ca. 2/5 of their length, subulate, not overlapping at base ; wings present, broad, narrowing to truncate at base, usually rather abruptly narrowing at apex, ca. 5 mm wide. Corolla white ; tube ca. 6-8 cm long, with distinct coronula of small knobs above anthers ; lobes broadly ovate, ca. 19 × 13 mm, acute. Anthers ca. 5 mm long, with thin and short appendix at apex. Capsule not seen.

DISTRIBUTION AND HABITAT : *T. vohimavensis* is endemic to the southeasternmost part of Madagascar, being known only from one collection from the Vohimavo peak at 308 m altitude. Flowering specimen seen from March.

NOTES : *T. vohimavensis* differs distinctly from *T. carinatus* by its white corolla, wide calyx wings and lanceolate and acuminate leaves, and, though only found once, must be recognized as a separate species. It is furthermore characterised by the wings along the stem, which are situated close to each other and below the point of attachment of the respective leaves, and not, as is usually the case, situated below but between the two leaves.

4. **Tachiadenus platypterus** Baker. — Pl. 7 ; 15, *C* (map).

J. Bot. 20 (in new ser. 11) : 172 (1882).

LECTOTYPE (here selected) : *Baron 218*, Madagascar, chiefly in Betsileo-land, (K ; iso-, P, one leaf only).

Moderately branched herb with woody base, 20-40 cm high or probably more ; branches erecto-patent to ± erect ; internodes rather short, usually shorter than leaves. Stem terete to subquadrangular, 4-lineolate ; lines situated close to each other in two opposite pairs. Leaves broadly ovate to elliptic to rarely narrowly elliptic, 3-6 × 0.5-2.5 cm, rounded to truncate at base, sessile, semi-amplexicaul, acute to obtuse, 3-nerved. Flowers usually rather many, solitary or in mono- or dichasial rather dense cymes ; pedicels short, ca. 5 mm long, straight to bent. Calyx 20-35 mm long, actinomorphic ; lobes coalescent 1/2-3/4 of their length, broadened in upper parts, not overlapping at base, acute to usually obtuse, with upper parts bent outwards ; wings present, usually broad, gradually narrowing at both ends, disappearing towards apex, accrescent (?) in fruit, 2-6 mm wide. Corolla white or violet ; tube 7.5-12 cm long, with distinct coronula of small knobs above anthers ; lobes broadly elliptic to almost rounded, 20-30 × 13-20 mm, acute to obtuse. Anthers 6-8 mm long, with short and thin or often broad appendix at apex. Capsule narrowly ovoid, gradually attenuate at apex, ca. 20 × 5 mm, slightly shorter than calyx, with two protruding mid-walls entirely coriaceous.

DISTRIBUTION AND HABITAT : *T. platypterus* occurs in the southern half of the mountains of central Madagascar. It has been collected in forest, savoka, savannahs and scrubland as well as in grassland and marshes, between 700 and 1850 m. Flowering specimens

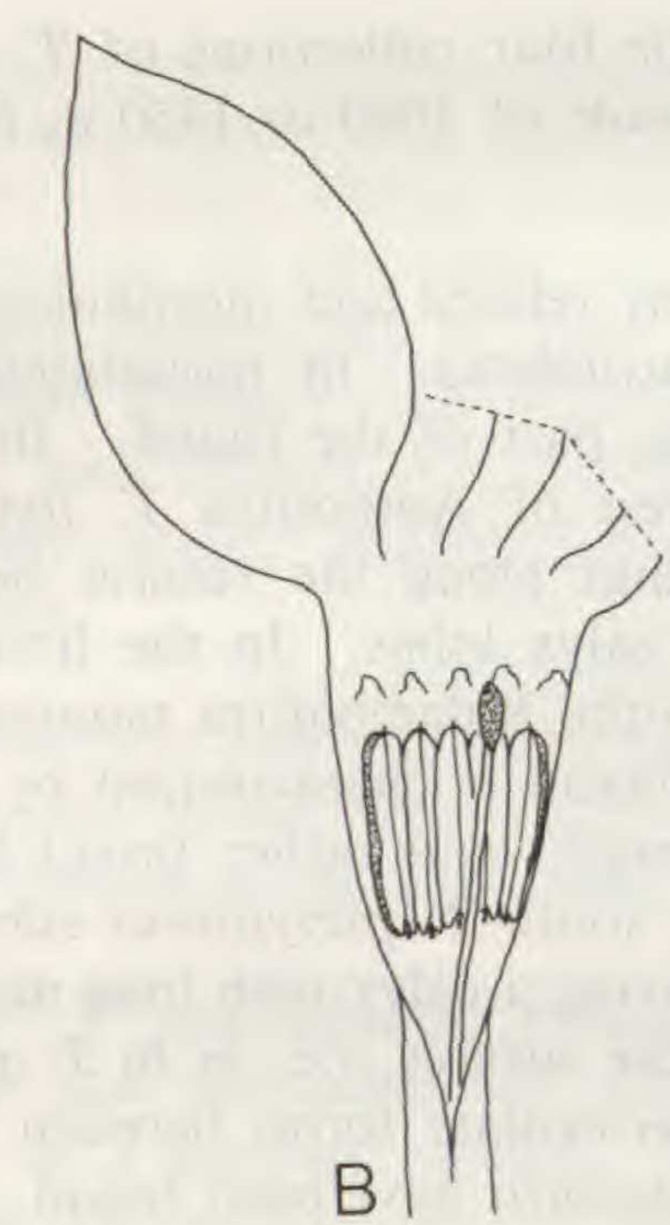
seen from August to February and April to May. The four collections of *T. platypterus* subsp. *angustialatus* are recorded from rocks at an altitude of 1000 to 1850 m flowering in November and December.

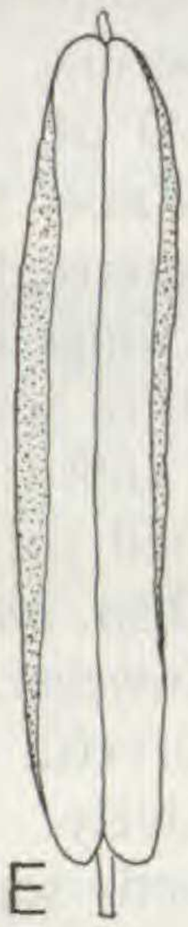
NOTES : *T. longiflorus* and *T. platypterus* are closely related and morphologically connected by the intermediate *T. platypterus* subsp. *angustialatus*. In mountainous central Madagascar these three taxa are distributed over a large part of the island. In the north from Lac Alaotra and south to the Itremo Massif west of Ambositra *T. longiflorus* is found, characterized by having a calyx with extra wings along the sutures between the sepals, and long (ca. 1/2 of the calyx length) narrow calyx lobes. In the Itremo mountains, sympatric with *T. longiflorus*, and southwards to the Kalambatitra mountains in the south, *T. platypterus* subsp. *platypterus* occurs. This taxon is characterized by short and broad calyx lobes (sepals coalescent > 2/3 of their length) and rather broad leaves. In southern Kalambatitra and the Ivakoany Massif further south *T. platypterus* subsp. *angustialatus* is found. This subspecies is characterized by having a calyx with long narrow lobes as in *T. longiflorus* but without the extra wings along the sutures, i.e. as in *T. platypterus* subsp. *platypterus*. In southern Kalambatitra some intermediate forms between *T. platypterus* subsp. *platypterus* and *T. platypterus* subsp. *angustialatus* have been found, e.g. specimens with slightly broadened and shortened calyx lobes. As discussed above, there are three taxa of which one, *T. platypterus* subsp. *angustialatus*, is obviously devoid of unique advanced characters (autapomorphies). However, *T. longiflorus* and *T. platypterus* subsp. *platypterus* are characterized by the unique extra calyx wings along the sutures between the sepals, and broad, flat calyx lobes, respectively. As, where contiguous, *T. longiflorus* and *T. platypterus* subsp. *platypterus* are distinctly separated, these two taxa are treated as species. On the contrary, *T. platypterus* subsp. *platypterus* and *T. platypterus* subsp. *angustialatus* are not morphologically distinctly separated where sympatric. However, being mostly allopatric and then always distinct, they are considered as subspecies.

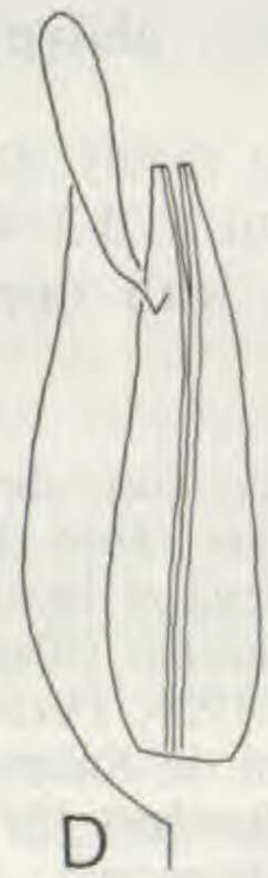
Tachiadenus platypterus Baker subsp. **platypterus**

Leaves broadly ovate to elliptic to rarely narrowly elliptic, 3-6 × 1-2.5 cm, obtuse. Calyx 20-30 mm long ; lobes coalescent 2/3-3/4 of their length, distinctly broadened in upper parts, acute to usually obtuse, with upper parts bent outwards ; wings present, usually broad, 2-6 mm wide.

SPECIMENS EXAMINED. — FIANARANTSOA : Env. de Ivohibe-Bara, ca. 1200 m, 1924, *Armand 67* (P) ; Env. de Ranotsara et Ihosy, 1963, *Bosser 18636* (P) ; Itremo, 1964, *Bosser 19594* (P) (somewhat deviating) ; Massif Ifandana, entre Ankaramena et Ihosy, 1300-1400 m, 1964, *Capuron 23503 SF* (P) ; Distr. Ambalavao, Canton d'Ambohimahamasina, village d'Ambohitrampanefy, 1100 m, 1955, *Cours 5008* (MO, P) ; Pic d'Ivohibe, 1500-1900 m, 1926, *Decary 5399* (P) ; 50 km E of Ambalavao, 1000 m, 1968, *Hoine 231* (K) ; Montagnes entre le col du Kalambatitra et la vallée de la Manambolo, affluent de l'Ianaivo (Ionaivo), ca. 1400 m, 1933, *Humbert 12115* (P, S) (both typical subsp. *platypterus* and individuals intermediate between the two subspecies) ; Montagnes à l'ouest d'Itremo, ouest Betsileo, pentes occidentales, 1500-1700 m, *Humbert 28323* (P) ; Nord du Kalambatitra, entre Ranotsara et Iakora, 700-900 m, 1973, *Morat 4244* (P) ; Vallée de l'Itomampy, 800 m, *Perrier 12647* (P, S) ; Distr. Ivohibe, Cant. Antambohobe, 1962, *Rakotoniaina 11986 RN* (P) ; Distr. Ambalavao, Cant. Vohitsaoka, 1955, *Rakotovao 7273 RN* (P) ; *Id.*, 1958, *9897 RN* (P) ; *Id.*, R.N. 5, 1954, *Rakotovao 6475 RN* (P, S) ; Distr. Ambalavao, Cant. Sendrisoa, 1958, *Rakotovao 9889 RN* (P) ; Distr. Ambalavao,







Pl. 7. — **Tachiadenus platypterus** : **A**, habit × 0.5 ; **B**, dissected upper part of flower × 1.5 ; **C**, **C'**, part of calyx (C = subsp. *platypterus* ; C' = subsp. *angustialatus*) × 1.5 ; **D**, flower in fruit with corolla and most of calyx removed × 1.5 ; **E**, anther × 6. (**A**, *Humbert 12115*, S ; B, C, E, *Bosser 18636* P ; *C'*, *Humbert 11973*, P ; D, *Capuron 23503 SF*, P).

Vohitsaoka, Betainamboa, 1950, *Razafindrakoto 2999 RN* (P) ; Near Taolana, ca. 1200 m, 1941, *Herb. Jard. Bot. Tananarive 4521* (P) ; Pied au l'Ambondrombe, 1941, 1200 m, *Herb. Jard. Bot. Tananarive 4563* (P) ; Inaninoma près d'Ambohimahanasina, 1941, *Herb. Jard. Bot. Tananarive 4720* (P).

INEXACT OR UNIDENTIFIED LOCALITIES : Chiefly in Betsileo-land, *Baron 218* (K, P) ; Ankafana, 1880, *Cowan s.n.* (P) ; Massif d'Andringitra, ca. 1600 m, 1922, *Perrier 14468* (P) ; Distr. Ambalavao, Cant. Ambohimanina, Ambohibary, 1950, *Razafindrakoto 2381 RN* (P).

Tachiadenus platypterus Baker subsp. **angustialatus** (Humbert) Klack., *stat. nov.*

— *Tachiadenus platypterus* BAKER var. *angustialatus* HUMBERT, Adansonia, ser. 2, 3 (3) : 349 (1963).

LECTOTYPE : *Humbert 11973*, Madagascar, Massif du Kalambatitra, Mont Analatsitendrika, 1750-1850 m, 1933 (P ; iso-, P, S) ; selected in herb.

Leaves narrowly elliptic to narrowly ovate, 3-6 × 0.5-1 cm, acute to obtuse. Calyx 25-35 mm long ; lobes coalescent 1/2-2/3 of their length, slightly broadened to usually subulate ; wings present, sometimes rather narrow but distinct, 0.5-2.5 mm wide.

SPECIMENS EXAMINED. — FIANARANTSOA : Bassin supérieur de l'Ianaivo (Ionaivo), affluent du Mananara, ca. 1000 m (ou Massif de l'Ivakoany, pentes NE, ca. 1100 m), 1928, *Humbert 6973* (P, S) ; Massif du Kalambatitra, mont Analatsitendrika, 1750-1850 m, 1933, *Humbert 11973* (P, S) ; Entre le col du Kalambatitra et la vallée de la Manambolo, affluent de l'Ianaivo (Ionaivo), 1200-1400 m, 1933, *Humbert 12093* (P) ; Centre-Sud, Massif de l'Ivakoany, pentes orientales du massif, 1250-1400 m, 1933, *Humbert 12269* (P).

5. **Tachiadenus longiflorus** Bojer ex Griseb. — Pl. 8 ; 15, *D* (map).

Gen. sp. Gent. 202 (1839).

LECTOTYPE (here selected) : *Bojer s.n.*, Hab. copiose in montib. prov. Emirna, Madagascar (K ; iso-, P).

Unbranched to moderately branched shrublet, 0.2-0.8 m high ; branches ± erect ; internodes usually shorter than leaves. Stem terete to subquadrangular, 4-lineolate ; lines situated close to each other in two opposite pairs. Leaves narrowly elliptic to narrowly ovate, 25-50 × 5-15 mm, gradually tapering at base to indistinct petiole to sessile, semi-amplexicaul, acute to obtuse, 3-nerved. Flowers usually rather few, solitary or in mono- or dichasial usually rather lax cymes ; pedicels short, 5-10 mm long, straight to bent. Calyx 25-40 mm long, actinomorphic ; lobes coalescent 2/5 to 1/2 of their length, subulate, not overlapping at base ; wings present and with one extra wing along each suture between sepals, rather narrow but distinct, gradually narrowing at both ends but the ones along the sutures often ± truncate or semi-sagittate at apex (i.e. at lobe sinuses), 0.5-1.5 mm wide. Corolla white, sometimes (?) with violet blotch at the very throat ; tube 7.0-12 cm long, with distinct coronula of small knobs above anthers ; lobes obovate to broadly ovate, 15-30 × 7-20 mm, acute to obtuse. Anthers 5.5-8 mm long, with short and thin or often broad appendix at apex. Capsule narrowly ovoid, gradually attenuate at apex, 16-18 × 4-6 mm, much shorter than calyx, with two protruding mid-walls entirely coriaceous.

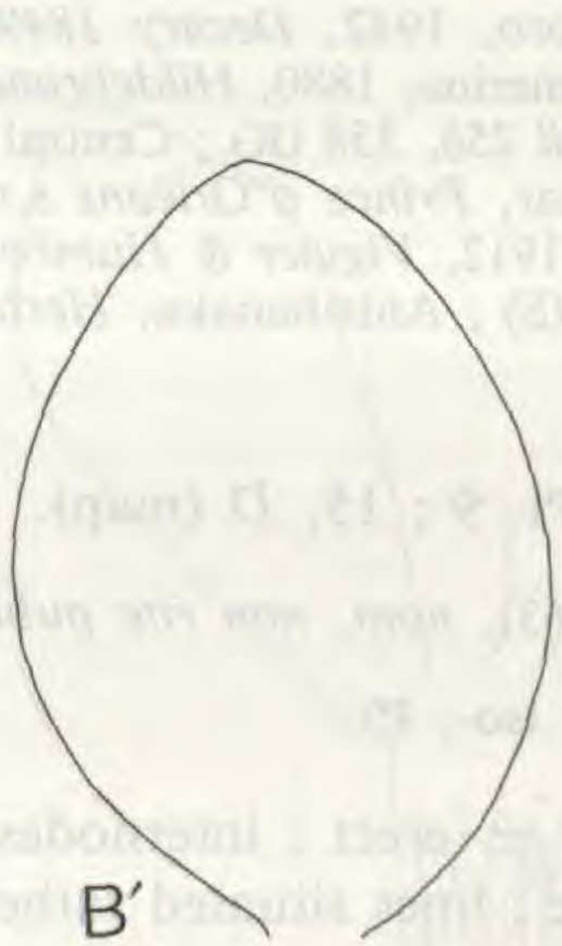
DISTRIBUTION AND HABITAT : *T. longiflorus* is distributed in mountainous Central Madagascar around Lac Alaotra in the north to the Ankaratra and Itremo Massifs in the south. It is recorded from 800-1800 m and grows in dry grass- and scrubland in clayey and stony soils. Flowering specimens seen from August to June.

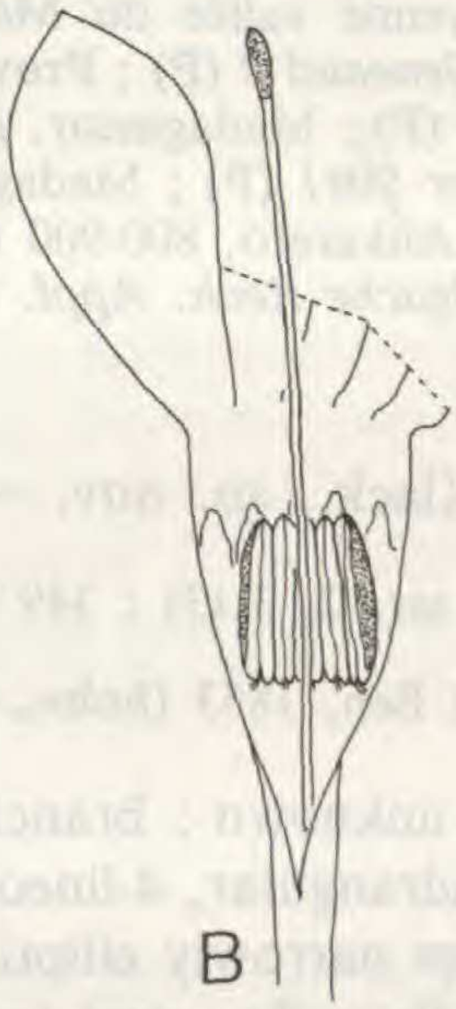
NOTES : The extra calyx wings of *T. longiflorus* are especially well developed in the northern part of the distribution area around Ambatondrazaka where they usually are semi-sagittate and sometimes even two along each suture. On the contrary, in the south (region Ambositra/Itremo) the extra wings are usually less prominent and tapering or occasionally even missing at some of the sutures. The latter specimens are morphologically close to *T. platypterus* subsp. *angustialatus* from the far south-east of the island, which, however, always totally lack the extra calyx wings. See also under Notes to *T. platypterus*.

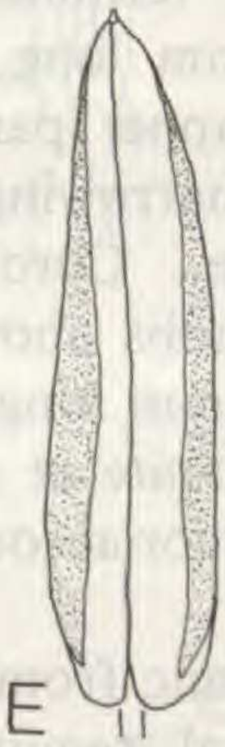
GRISEBACH (1839 : 202) cited in the protologue collections of *Lyall* and of *Bojer* (« *Boyer* ») in *Herb. Hooker*. I have chosen as lectotype the BOJER specimen which was probably also the base of BOJER's manuscript name.

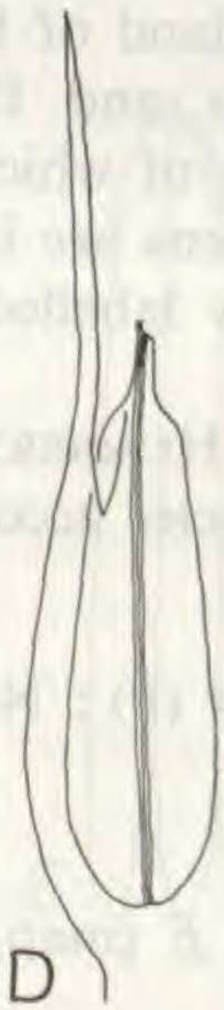
SPECIMENS EXAMINED. — MAJUNGA : Distr. Tsaratanana, Cant. Andriamena, Telomita, Androfia, 1100 m, 1964, *Service Eaux Forêts Madagascar 21875 SF* (P). — TAMATAVE : Ambatondrazaka, Manaka-Est, 1954, *Botoalina 6975 RN* (P, S) ; Sud de Moramanga, 1930, *Decary 6976* (P, S) ; Moramanga, 1930, *Decary 7228* (P) ; Ambatondrazaka, 1941, *Decary 16456* (BM, P) ; Lac Alaotra, entre Menasaka et Ambodiriana, bords du Maningory, 1944, *Homolle 516* (P) ; Ca. 48 km S Ambatondrazaka, 2 km S Beforo on the road to Moramanga, 850 m, 1978, *Jonsson 1020* (P) ; Distr. Ambatondrazaka, Manakambahiny Est, 1959, *Rakatovao 10521 RN* (P) ; Canton Manakambahiny Est, Distr. Ambatondrazaka, Ankarongana, 1949, *Ramanantsoavina 1794 RN* (P, S) ; Distr. Ambatondrazaka, Manakambahiny Est, 1948, *Ratoto M de D & Ramarokoto 1546* (P) ; Prov. d'Andovoranto, Distr. de Moramanga, env. de Moramanga, 900 m, 1912, *Viguier & Humbert 1031* (P) ; Andranokobaka, Moramanga, 1951, *Service Eaux Forêts Madagascar 3240 SF* (P) ; Andranokobaka, 1951, *s. coll. no. 3240* (P, S). — TANANARIVE : Tananarive, 1903, *Bernard s.n.* (P) ; Ambatolaona, 1937, *Boiteau 2397* (P) ; Vallée de Soarina, P.K. 23, route de Tamatave, 1961, *Bosser 14868* (MO) ; Angavokely 30 km E Tananarive, 1949, *Capuron 72 SF* (P) ; Ambatolaona, 1921, *Decary 580* (P) ; Ambohimanga, 1921, *Decary 653* (P) ; Ambohimanga, près de Tananarive, 1928, *Decary 6151* (K, P) ; Ilafy, 1917, *Decary s.n.* (P) ; Tsimbazaza, 1917, *Decary s.n.* (P) ; R.N. 2, E of Antananarivo at second crossing of the Ampasibe River, 1985, *Dorr 3681* (MO) ; Env. d'Arivonimamo, ca. 8 km sur la route d'Ahitrambo, 1957, *Descoings 2885* (MO) ; Rock outcrops NW of Behenjy on road from Antananarivo to Antsirabe, 1986, *Dorr, Barnett & Rakotozafy 4568* (MO) ; Distr. Ankazobe, Cant. Manolaza, Manankazo, forêt d'Ambohitantely, 1948, *Jean de Dieu 171 RN* (P) ; Entre Arivonimamo et Soamananety, 1960, *Peltier 1818* (P) ; Andranavelona, route N4, 1963, *Peltier 4469* (P) ; Ambohimanga, Soavinimerina, 1967, *Rosamolson 6* (P) ; Tananarive, Ambohimanga 1921, *Waterlot 61* (P) ; Ilafy, 1905, *Herb. d'Alleizette 378* (P) ; Mahitsy, 1942, *Herb. Jard. Bot. Tananarive 5038* (P). — FIANARANTSOA : 46 km E of Ambatofinandrahana (Fiandrahanom), 1350 m, 1975, *Croat 29509* (MO) ; Along Route 35, 54 km E of Ambatofinandrahana (Finandrohana), 1300 m, 1975, *Croat 29676* (MO) ; Massif de l'Itremo, vicinity of Col de Itremo, 1500-1685 m, 1975, *Croat 29870* (MO) ; Env. de Ambatofinandrahana, 1600-1800 m, 1938, *Decary 13058, 13243* (P) ; Ambositra, bois de Tapia, 1942, *Decary 17267* (P) ; Ambatofinandrahana, 1942, *Decary 17389* (P) ; Montagnes à l'ouest d'Itremo, ouest Betsileo, 1500-1700 m, 1955, *Humbert 30028* (P, S) ; Environs d'Ambatofinandrahana, Betsileo, 1400-1500 m, *Humbert & Capuron 28127* (P, S) ; Dt. Fandriana, Sandrandahy, 1960, *Peltier 2221* (P) ; Soanieranana, col d'Antoetra, Dt. d'Ambositra, 1960, *Peltier 2232* (P) (somewhat deviating) ; Env. d'Ambositra, 1400 m, 1911, *Perrier 9044* (P) ; Mantasoa, 1905, *Académie Malgache s.n.* (P) ; Ankatso, 1942, *Herb. Jard. Bot. Tananarive s.n.* (P).

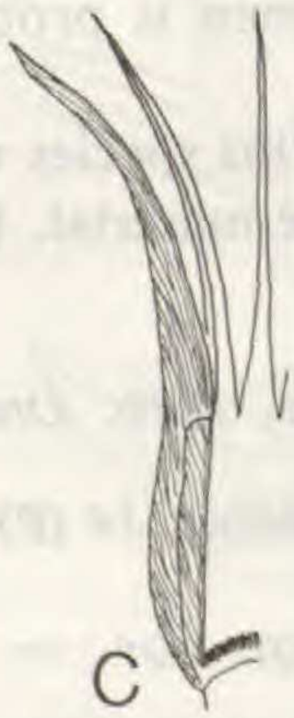
INEXACT OR UNIDENTIFIED LOCALITIES : Chiefly in Betsileo-land, *Baron 130, 163* (K) ; Central Madagascar, *Baron 384* (K, P), *s.n.* (P) ; In altis montibus Madagascar, *Blackburn s.n.* (K) ; Ferme séricole IMRA, Mahabo, 1970, *Boiteau 2001* (P, S) ; Prov. Imerina (Emerinae, Emirna), *Bojer s.n.* (K, P) ; Imerina, 1887, *Campenon s.n.* (P) ; Sampatra, 1889, *Catat 1705* (P) ; Distr. Ambatondrazaka,

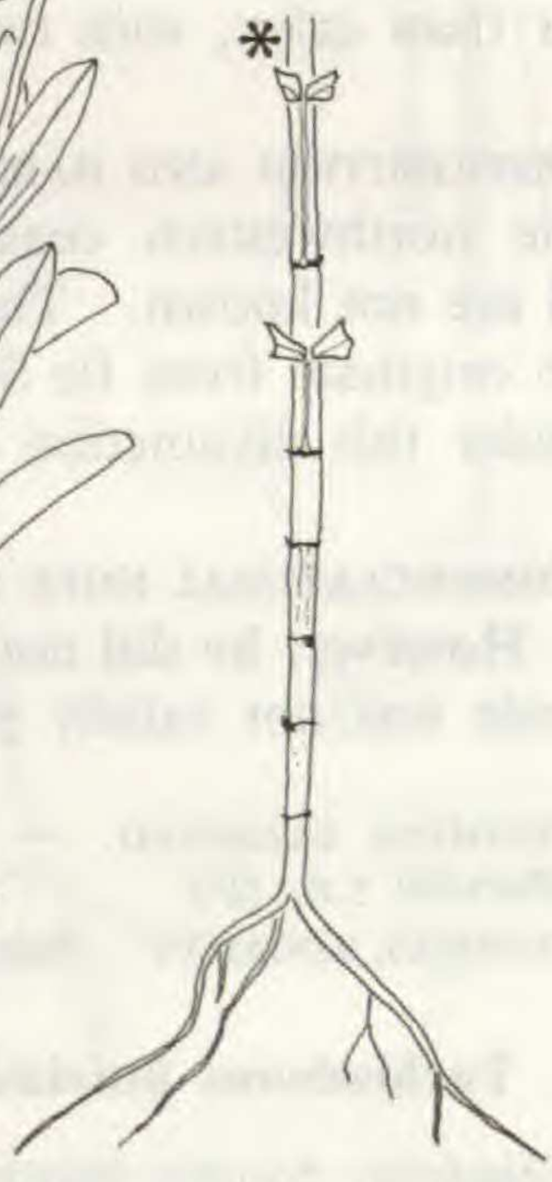












Pl. 8. — **Tachiadenus longiflorus** : **A**, habit × 0.5 ; **B**, dissected upper part of flower (B′ = petal lobe from different collections) × 1.5 ; **C**, part of calyx × 1.5 ; **D**, flower in fruit with corolla and most of calyx removed × 1.5 ; **E**, anther × 6. (A-C, E, *Boiteau 2001*, S ; B′, *Ramananboavina 1794 RN*, S ; D, *Botoalina 6975 RN*, S).

Ankaroka, 1300 m, 1938, *Cours 29* (P) ; Moyenne vallée du Mangoro, 1942, *Decary 18498* (P) ; Madagascar, *Elliot 1939* (K, P) ; *S. loc.*, 1892, *Geneaud 2* (P) ; Prov. Imerina, 1880, *Hildebrandt 3492* (K, P) ; Tamatave, 1887, *Le Myre de Vilers s.n.* (P) ; Madagascar, *Lyall 258, 358* (K) ; Central Madagascar, *Parker s.n.* (K) ; Mangoro, 1912, *Perrier 9041* (P) ; Madagascar, *Prince d'Orléans s.n.* (P) ; Prov. d'Andovoranto, Distr. de Moramanga, d'Ankarefo, 800-900 m, 1912, *Viguier & Humbert 1184* (P) ; Plateau de Soavenimerina, 1967, *Inst. Malgache Rech. Appl. 6* (S) ; Antsihanaka, *Herb. Jard. Bot. Tananarive s.n.* (P).

6. **Tachiadenus pervillei** Humbert ex Klack., *sp. nov.* — Pl. 9 ; 15, *D* (map).

— *Tachiadenus pervillei* Humbert, Adansonia, ser. 2, 3 (3) : 349 (1963), *nom. non rite publ.*

Type : *Pervillé s.n.*, Madagascar, Ile Nossi Beh, 1853 (holo-, P ; iso-, P).

Moderately branched shrublet, height unknown ; branches ± erect ; internodes much shorter than leaves. Stem terete to subquadrangular, 4-lineolate ; lines situated rather close to each other in two opposite pairs. Leaves narrowly elliptic, ca. 6-10 × 1.5-2.5 cm, attenuate at base to ± distinct petiole or subsessile, semi-amplexicaul, acute, 3(-5)-nerved. Flowers few, in mono- or dichasial cymes or solitary in terminal position in forks of branches ; pedicels short, ca. 5 mm long. Calyx 28-37 mm long, actinomorphic ; lobes coalescent ca. 1/2 of their length, slightly broadened at upper parts, not overlapping at base, acute ; wings present, narrow to broad, gradually narrowing at both ends, disappearing towards apex, accrescent (?) in fruit, 1-5 mm wide. Corolla : colour unknown ; tube 9-13 cm long, with a ± distinct coronula of small knobs above anthers ; lobes obovate, ca. 27 × 13 mm, acute to ± obtuse. Anthers ca. 8 mm long, with a thin and short appendix at apex. Capsule narrowly ovate, gradually attenuate at apex, ca. 20 × 5 mm, shorter than calyx, with two protruding mid-walls entirely coriaceous.

Distribution and habitat : *T. pervillei* is a local endemic from the island of Nossi Be off the northwestern coast of Madagascar. Its ecological requirements and flowering period are not known. There are two collections of Boivin of this species of which one is said to originate from Ile Sainte-Marie on the east coast. The two specimens are identical. I consider this disjunction doubtful and the specimen is probably wrongly labelled.

Nomenclatural note : A latin description of this species was given by Humbert (1963 : 349). However, he did not assign any specific type material, hence the species according to the Code was not validly published (Article 37.1).

Specimens examined. — Diego-Suarez : Nossi Be, *Herb. Drake, Boivin 19* (P) ; Nossi Beh, 1853, *Pervillé s.n.* (P).

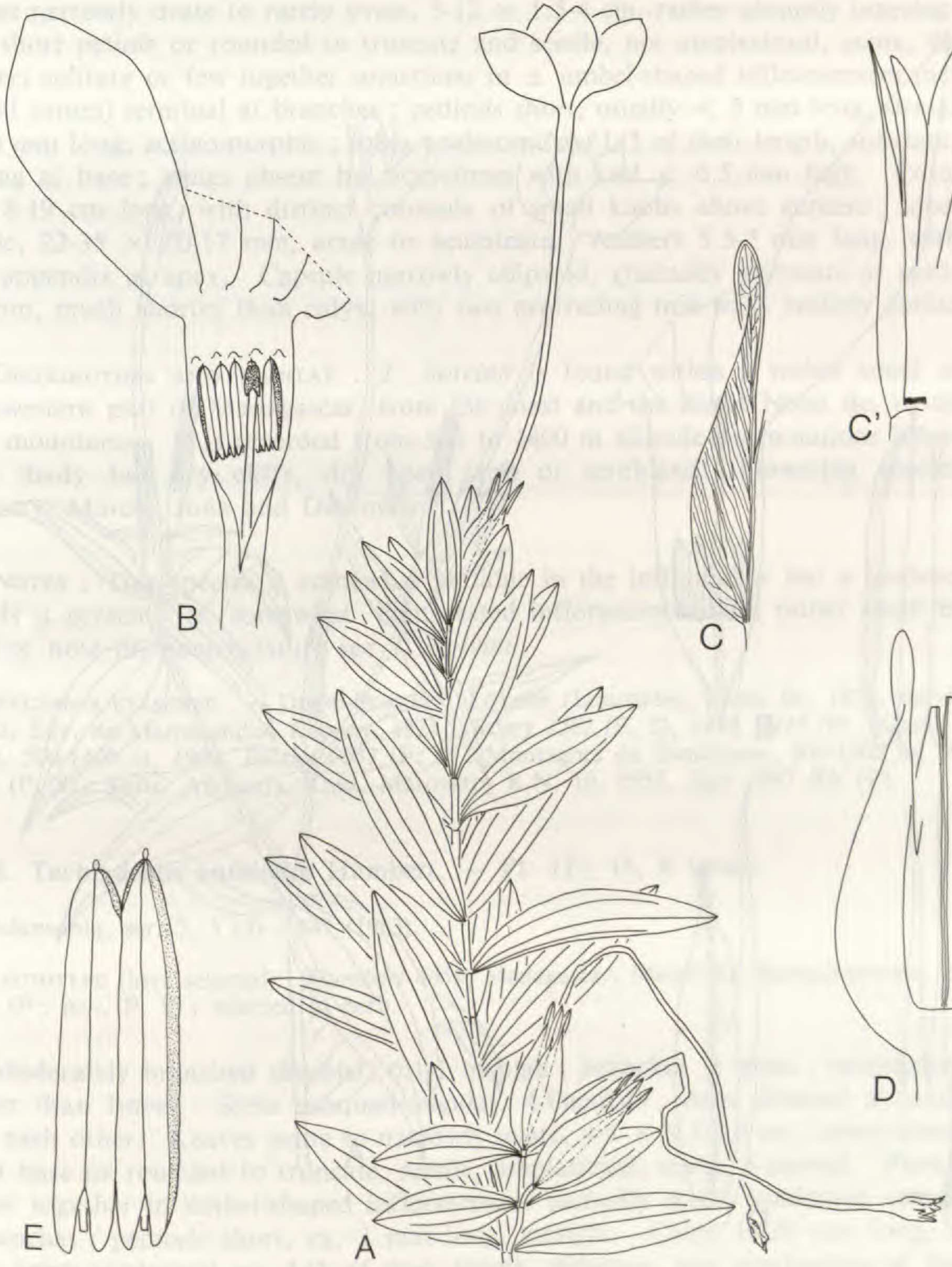
Doubtful locality : Sainte-Marie, *Herb. Drake, Boivin 14* (P).

7. **Tachiadenus boivinii** Humbert ex Klack., *sp. nov.* — Pl. 10 ; 15, *E* (map).

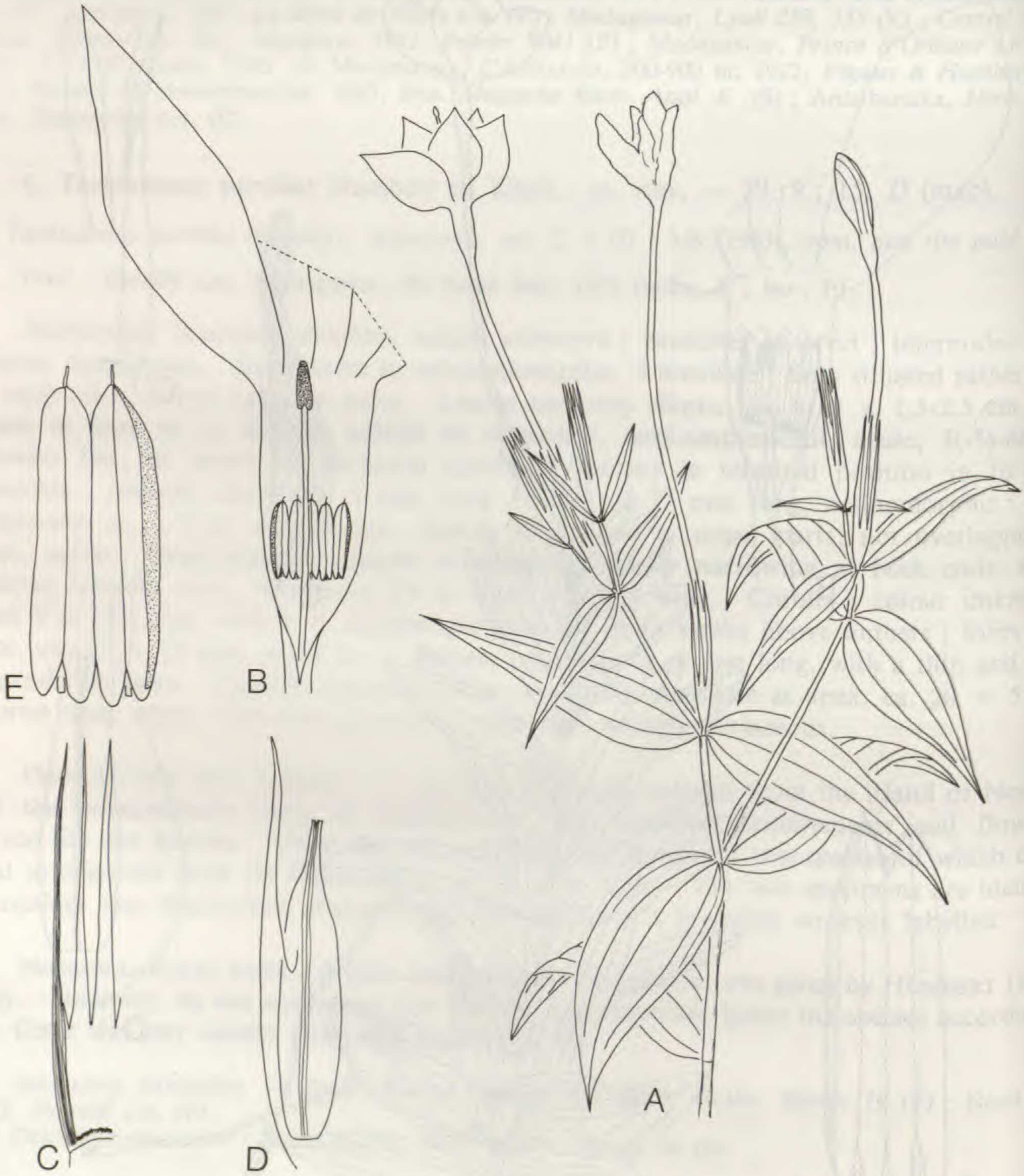
— *Tachiadenus boivinii* Humbert, Adansonia, ser. 2, 3 (3) : 349 (1963), *nom. non rite publ.*

Type : *Perrier de la Bâthie 9053*, Madagascar, Massif de Manongarivo (holo-, P ; iso-, P, S).

Moderately branched shrublet, up to 1.5 m high ; branches ± erect ; internodes usually shorter than leaves. Stem terete, 4-lineolate ; lines situated rather close to each other in



Pl. 9. — **Tachiadenus pervillei** : **A**, habit × 0.5 ; **B**, dissected upper part of flower × 1.5 ; **C**, part of calyx (C′ = calyx almost without wings from the same collection) × 1.5 ; **D**, flower in fruit with corolla and most of calyx removed × 1.5 ; **E**, anther × 6. (A-C, E, *Pervillé s.n.*, 1853, P ; D, *Boivin 19*, P).



Pl. 10. — **Tachiadenus boivinii** : **A**, habit × 0.5 ; **B**, dissected upper part of flower × 1.5 ; **C**, part of calyx × 1.5 ; **D**, flower in fruit with corolla and most of calyx removed × 1.5 ; **E**, anther × 6. (**A**, *Decary 1581*, P ; B, C, E, *Decary 1581*, S ; D, *Perrier de la Bâthie 9053*, S).

two opposite pairs, sometimes distinct only immediately below leaves or almost absent. Leaves narrowly ovate to rarely ovate, 5-12 × 1.5-4 cm, rather abruptly tapering at base to very short petiole or rounded to truncate and sessile, not amplexicaul, acute, 3(-5)-nerved. Flowers solitary or few together sometimes in ± umbel-shaped inflorescences (actually condensed cymes) terminal at branches ; pedicels short, usually < 5 mm long, straight. Calyx 25-40 mm long, actinomorphic ; lobes coalescent ca. 1/3 of their length, subulate, not overlapping at base ; wings absent but sometimes with keel < 0.5 mm high. Corolla white ; tube 8-19 cm long, with distinct coronula of small knobs above anthers ; lobes ovate to elliptic, 22-35 × 10-17 mm, acute to acuminate. Anthers 5.5-7 mm long, with thin and long appendix at apex. Capsule narrowly ellipsoid, gradually attenuate at apex, 20-25 × 4-5 mm, much shorter than calyx, with two protruding mid-walls entirely coriaceous.

DISTRIBUTION AND HABITAT : *T. boivinii* is found within a rather small area in the northwestern part of Madagascar, from the coast and the island Nossi Be, to the Tsaratanana mountains. It is recorded from 500 to 1400 m altitude (no notations from Nossi Be) from shady but dry cliffs, dry open land or scrubland. Flowering specimens from February, March, June and December.

NOTES : This species is somewhat variable in the infloresence but a tendency towards umbels is present, i.e. somewhat compressed inflorescences with rather small bracts.
For note on nomenclature see *T. boivinii*.

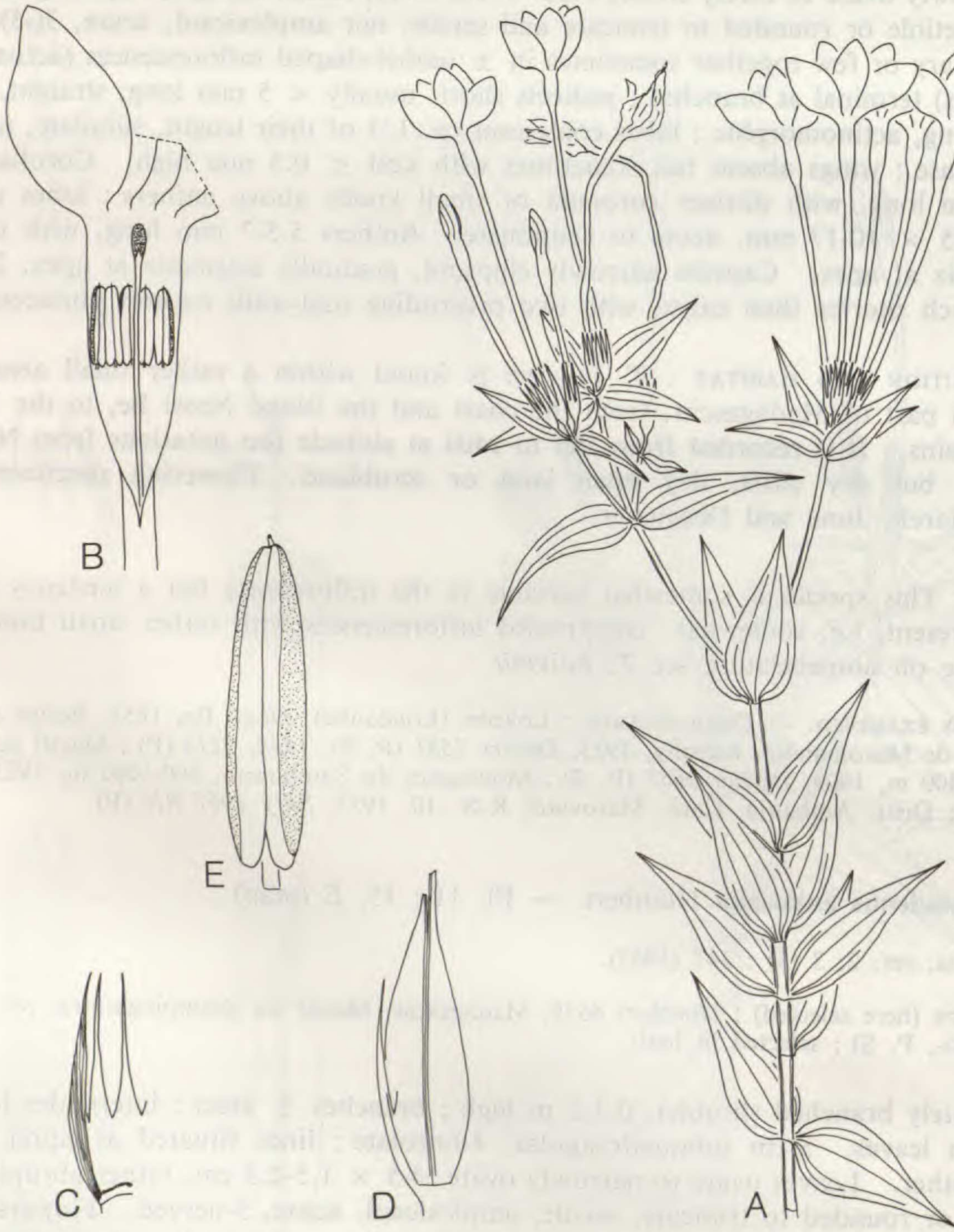
SPECIMENS EXAMINED. — DIEGO-SUAREZ : Lokobe (Loucoube), Nossi Be, 1851, *Boivin s.n.* (P) ; Bejofo, Env. de Maromandia, Kapany, 1923, *Decary 1581* (P, S), *1438, 2219* (P) ; Massif de Manongarivo, 500-1400 m, 1909, *Perrier 9053* (P, S) ; Montagnes du Sambirano, 600-1000 m, 1923, *Perrier 15532* (P, S) ; Distr. Ambanja, Cant. Marovato, R.N. 10, 1953, *Safy 4967 RN* (P).

8. **Tachiadenus antaisaka** Humbert. — Pl. 11 ; 15, *E* (map).

Adansonia, ser. 2, 3 (3) : 347 (1963).

LECTOTYPE (here selected) : *Humbert 6659*, Madagascar, Massif du Beampingaratra, col de Vohipaha, (P ; iso-, P, S) ; selected in herb.

Moderately branched shrublet, 0.1-1 m high ; branches ± erect ; internodes longer or shorter than leaves. Stem subquadrangular, 4-lineolate ; lines situated at equal distance from each other. Leaves ovate to narrowly ovate, 4-5 × 1.5-2.5 cm, rather abruptly tapering at base or rounded to truncate, sessile, amplexicaul, acute, 5-nerved. Flowers solitary or few together in umbel-shaped inflorescences (actually much condensed cymes) terminal at branches ; pedicels short, ca. 3 mm long, straight. Calyx 15-20 mm long, actinomorphic ; lobes coalescent ca. 1/3 of their length, subulate, not overlapping at base ; wings usually absent but sometimes with keel or narrow wing < 1 mm wide. Corolla white ; tube 7-10 cm long, without coronula ; lobes ovate, ca. 15-25 × 7-15 mm, acute to ± obtuse. Anthers 5-6 mm long, with a thin and short appendix at apex. Capsule narrowly ovoid to narrowly ellipsoid, gradually attenuate at apex, ca. 15 × 5 mm, longer than calyx, with two protruding mid-walls partly membranaceous.



Pl. 11. — **Tachiadenus antaisaka** : **A**, habit × 0.5 ; **B**, dissected upper part of flower × 1.5 ; **C**, part of calyx × 1.5 ; **D**, flower in fruit with corolla and most of calyx removed × 1.5 ; **E**, anther × 6. (A-E, *Humbert 13538*, S).

DISTRIBUTION AND HABITAT : *T. antaisaka* is a local endemic known only from the Beampingaratra mountains in the very southeastern part of Madagascar. It is recorded from forest from 1100 to 2000 m altitude. Flowering specimens seen from October to January.

NOTES : This species is characterized by its sessile amplexicaul 5-nerved leaves. It is the only species with a calyx covered by small epidermal papillae (lens !). See also Notes to *T. umbellatus*.

SPECIMENS EXAMINED. — TULEAR : Massif de l'Andohahelo, 1800-1979 m, 1928, *Humbert 6180* (P) ; *Id.*, 1700-1975 m, 1934, *Humbert 13587* (P) ; Massif du Beampingaratra, col de Vohipaha, 1100-1400 m, 1928, *Humbert 6659* (P, S).

INEXACT OR UNIDENTIFIED LOCALITIES : Mont Itrafanaomby (Ankazondrano) et ses contreforts S-W (haut Mandrare), 1700-1963 m, 1933, *Humbert 13538* (P, S).

9. **Tachiadenus umbellatus** Klack., *sp. nov.* — Pl. 12 ; 15, *E* (map).

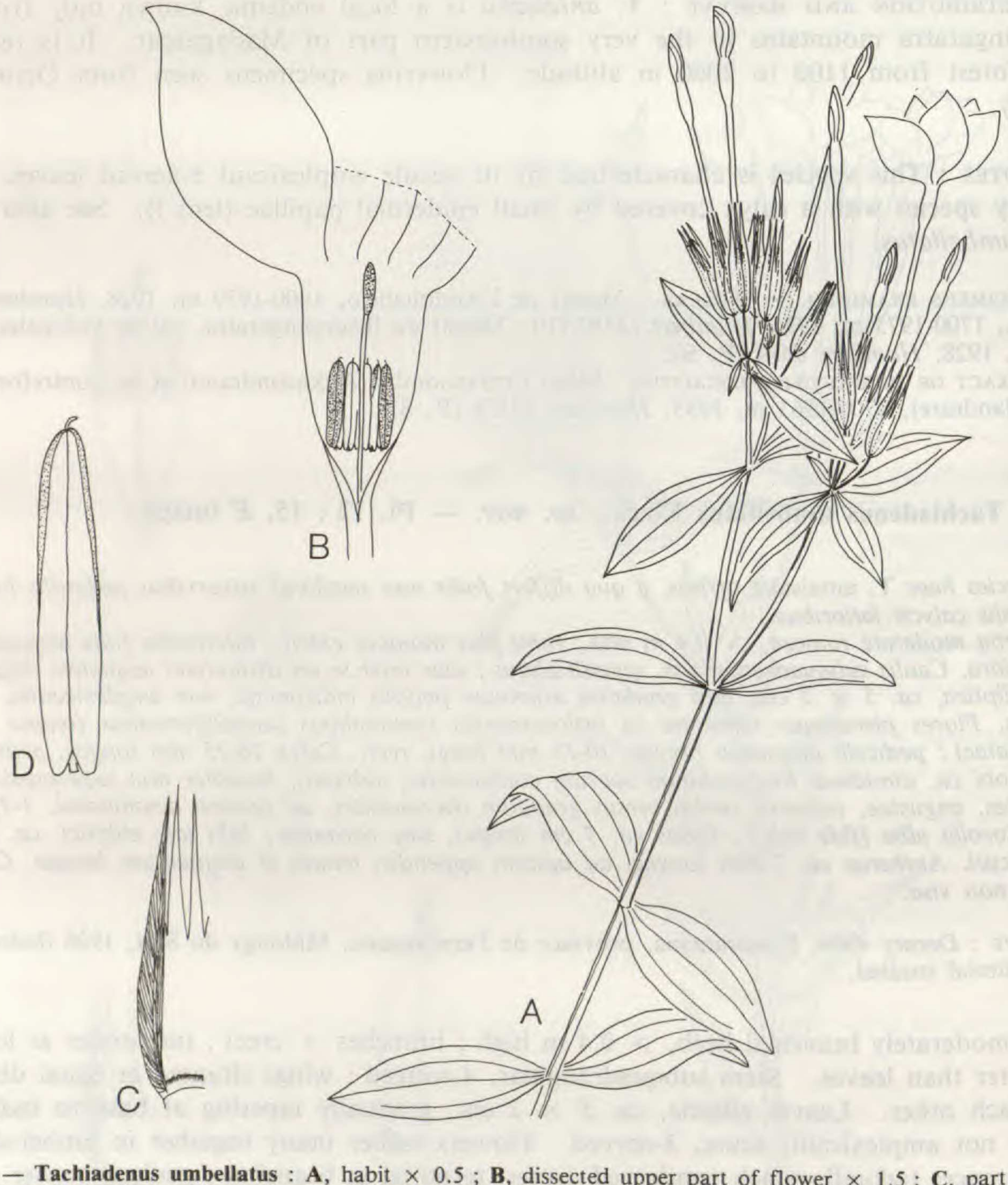
Species haec T. antaisaka *affinis, a qua differt foliis non sessilibus trinervibus pedicellis longioribus et alis calycis latioribus.*

Herba moderate ramosa, > 0,4 m alta ; rami plus minusve erecti ; internodia folia aequantia vel eis breviora. Caulis subquadrangularis, quandrialatus ; alae inter se ad distantiam aequalem dispositae. Folia elliptica, ca. 5 × 2 cm, basi gradatim attenuata petiolis indistinctis, non amplexicaulia, acuta, trinervia. Flores plerumque numerosi in inflorescentiis terminalibus umbelliformibus (reapse cymae condensatae) ; pedicelli aliquanto breves, 10-15 mm longi, recti. Calyx 20-25 mm longus, actinomorphus ; lobi ca. dimidium longitudinum suarum coalescentes, subulati, basaliter non superpositi ; alae praesentes, angustae, extremia ambo versus gradatim decrescentes, ad apicem acuminatae, 1-1,5 mm latae. Corolla alba (fide coll.) ; tubus ca. 7 cm longus, sine coronula ; lobi late elliptici, ca. 2,5 × 2 cm, acuti. Antherae ca. 7 mm longae, ad apicem appendici tenues et aliquantum longae. Capsula matura non visa.

TYPE : *Decary 4966*, Fianarantsoa, province de Farafangana, Midongy du Sud, 1926 (holo-, P) ; only material studied.

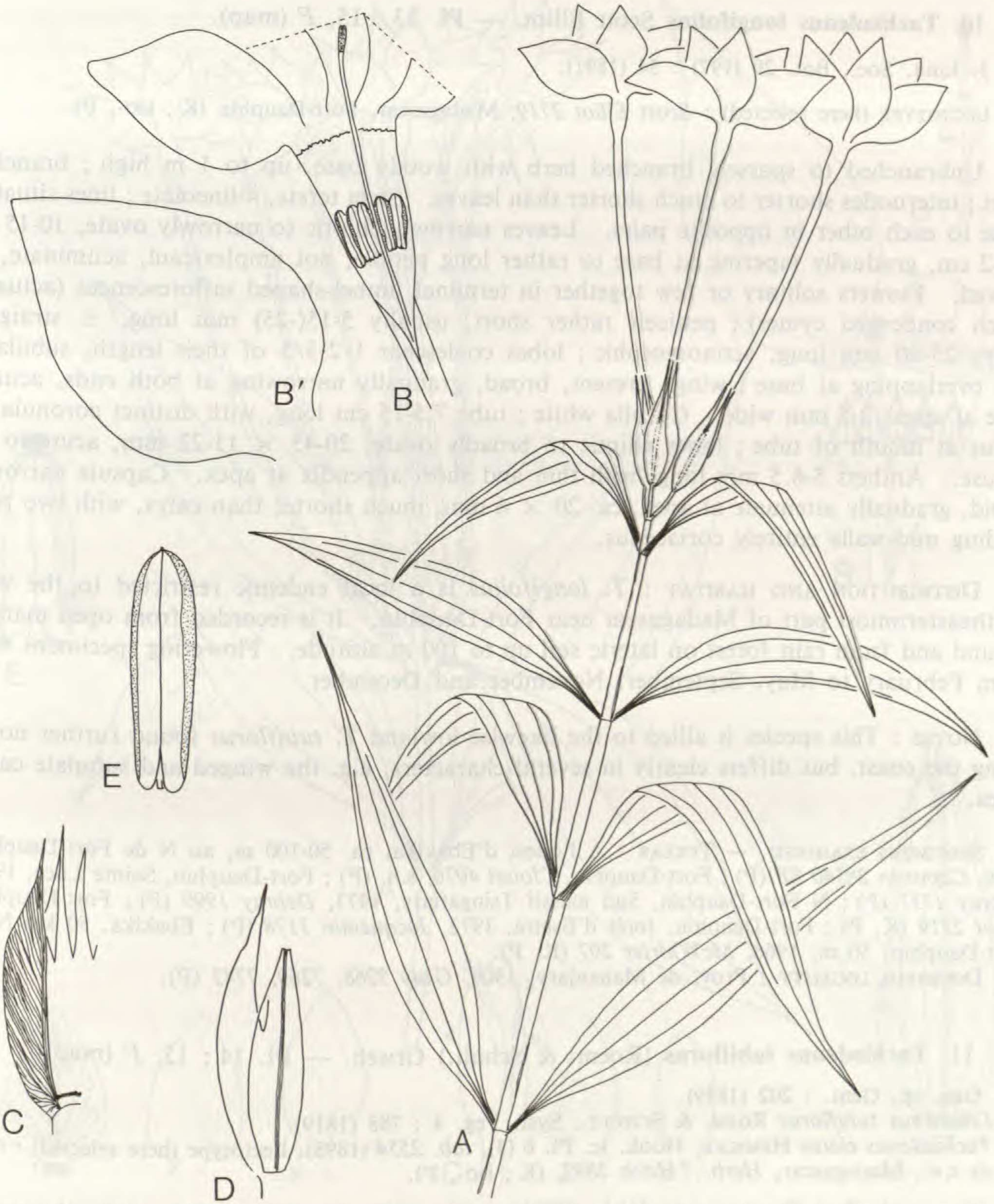
A moderately branched herb, > 0.4 m high ; branches ± erect ; internodes as long as or shorter than leaves. Stem subquadrangular, 4-winged ; wings situated at equal distance from each other. Leaves elliptic, ca. 5 × 2 cm, gradually tapering at base to indistinct petiole, not amplexicaul, acute, 3-nerved. Flowers rather many together in umbel-shaped inflorescences (actually much condensed cymes) terminal at branches ; pedicels rather short, 10-15 mm long, straight. Calyx 20-25 mm long, actinomorphic ; lobes coalescent ca. 1/2 of their length, subulate, not overlapping at base ; wings present, narrow, gradually narrowing at both ends, acuminate at apex, 1-1.5 mm wide. Corolla white (*fide* coll.) ; tube ca. 7 cm long, without coronula ; lobes broadly elliptic, ca. 2.5 × 2 cm, acute. Anthers ca. 7 mm long, with thin and rather long appendix at apex. Capsule (mature) not seen.

DISTRIBUTION AND HABITAT : *T. umbellatus* is endemic to the Massif du Midongy in the southeastern part of Madagascar. It is known only from the type collection found in exposed wet places. Flowering specimen seen from August.



Pl. 12. — **Tachiadenus umbellatus** : **A**, habit × 0.5 ; **B**, dissected upper part of flower × 1.5 ; **C**, part of calyx × 1.5 ; **D**, anther × 6. (A-D, *Decary 4966*, P).

Notes : This species is allied to *T. antaisaka*. Both these taxa are found in the south-eastern part of the island and both seem to be local endemics. *T. umbellatus* differs by its 3-nerved elliptic somewhat petiolated leaves, its longer pedicels and broader calyx wings. It is considered, that, though it has been found only once, the relatively large differences with *T. antaisaka* as well as all other species of *Tachiadenus*, require this taxon to be described as a new species.



Pl. 13. — **Tachiadenus longifolius** : **A**, habit × 0.5 ; **B**, dissected upper part of flower (B′ = petal lobe from different individual of same collection) × 1.5 ; **C**, part of calyx × 1.5 ; **D**, flower in fruit with corolla and most of calyx removed (somewhat immature) × 1.5 ; **E**, anther × 6. (A, *Capuron 28340 SF*, P ; B, C, E, *McWhirter 207*, P ; D, *Jacquemin 1178*, P).

10. **Tachiadenus longifolius** Scott Elliot. — Pl. 13 ; 15, *F* (map).

J. Linn. Soc., Bot. 29 (197) : 34 (1891).

LECTOTYPE (here selected) : *Scott Elliot 2719*, Madagascar, Fort-Dauphin (K ; iso-, P).

Unbranched to sparsely branched herb with woody base, up to 1 m high ; branches erect ; internodes shorter to much shorter than leaves. Stem terete, 4-lineolate ; lines situated close to each other in opposite pairs. Leaves narrowly elliptic to narrowly ovate, 10-15 × 1.5-2 cm, gradually tapering at base to rather long petiole, not amplexicaul, acuminate, 3-nerved. Flowers solitary or few together in terminal umbel-shaped inflorescences (actually much condensed cymes) ; pedicels rather short, usually 5-15(-25) mm long, ± straight. Calyx 25-40 mm long, actinomorphic ; lobes coalescent 1/2-3/5 of their length, subulate, not overlapping at base ; wings present, broad, gradually narrowing at both ends, acuminate at apex, 2-5 mm wide. Corolla white ; tube 7.5-15 cm long, with distinct coronula of callus at mouth of tube ; lobes elliptic to broadly ovate, 20-45 × 11-22 mm, acute to ± obtuse. Anthers 5-6.5 mm long, with thin and short appendix at apex. Capsule narrowly ovoid, gradually attenuate at apex, ca. 20 × 6 mm, much shorter than calyx, with two protruding mid-walls entirely coriaceous.

DISTRIBUTION AND HABITAT : *T. longifolius* is a local endemic restricted to the very southeasternmost part of Madagascar near Fort-Dauphin. It is recorded from open marshy ground and from rain forest on lateric soil up to 100 m altitude. Flowering specimens seen from February to May, September, November and December.

NOTES : This species is allied to the likewise lowland *T. tubiflorus* found further north along the coast, but differs clearly in several characters, e.g. the winged and subulate calyx lobes.

SPECIMENS EXAMINED. — TULEAR : A l'ouest d'Ebakika, ca. 50-100 m, au N de Fort-Dauphin, 1968, *Capuron 28340 SF* (P) ; Fort-Dauphin, *Cloisel 4076, s.n.* (P) ; Fort-Dauphin, Sainte Luce, 1972, *Debray 1737* (P) ; N Fort-Dauphin, Sud massif Tsingafiafy, 1973, *Debray 1999* (P) ; Fort-Dauphin, *Elliot 2719* (K, P) ; Fort-Dauphin, forêt d'Esetra, 1972, *Jacquemin 1178* (P) ; Ebakika, 50 km N of Fort-Dauphin, 50 m, 1968, *McWhirter 207* (K, P).

DOUBTFUL LOCALITY : Prov. de Mananjary, 1909, *Geay 7268, 7269, 7742* (P).

11. **Tachiadenus tubiflorus** (Roem. & Schult.) Griseb. — Pl. 14 ; 15, *F* (map).

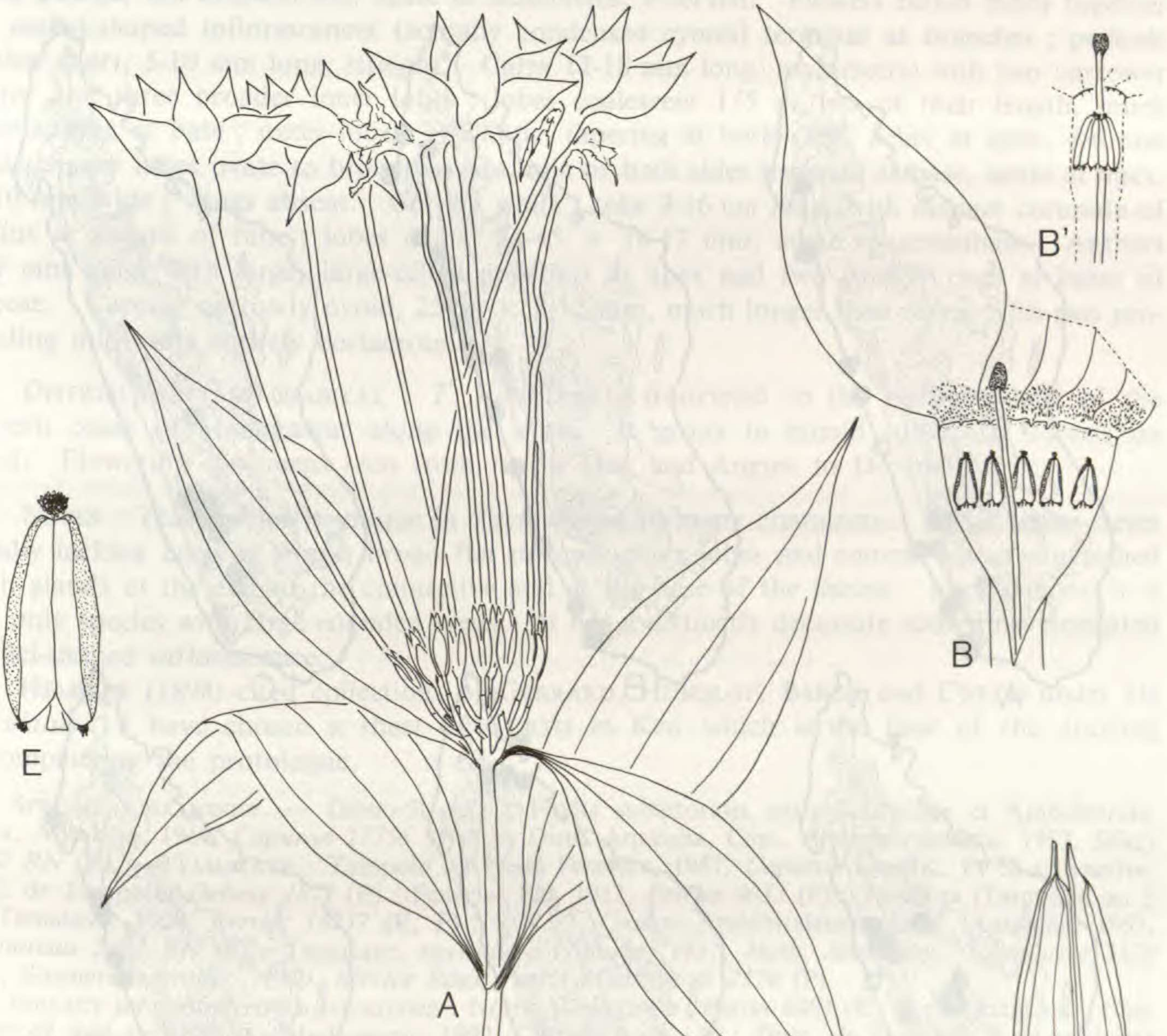
Gen. sp. Gent. : 202 (1839).

— *Lisianthus tubiflorus* ROEM. & SCHULT., Syst. Veg. 4 : 788 (1819).

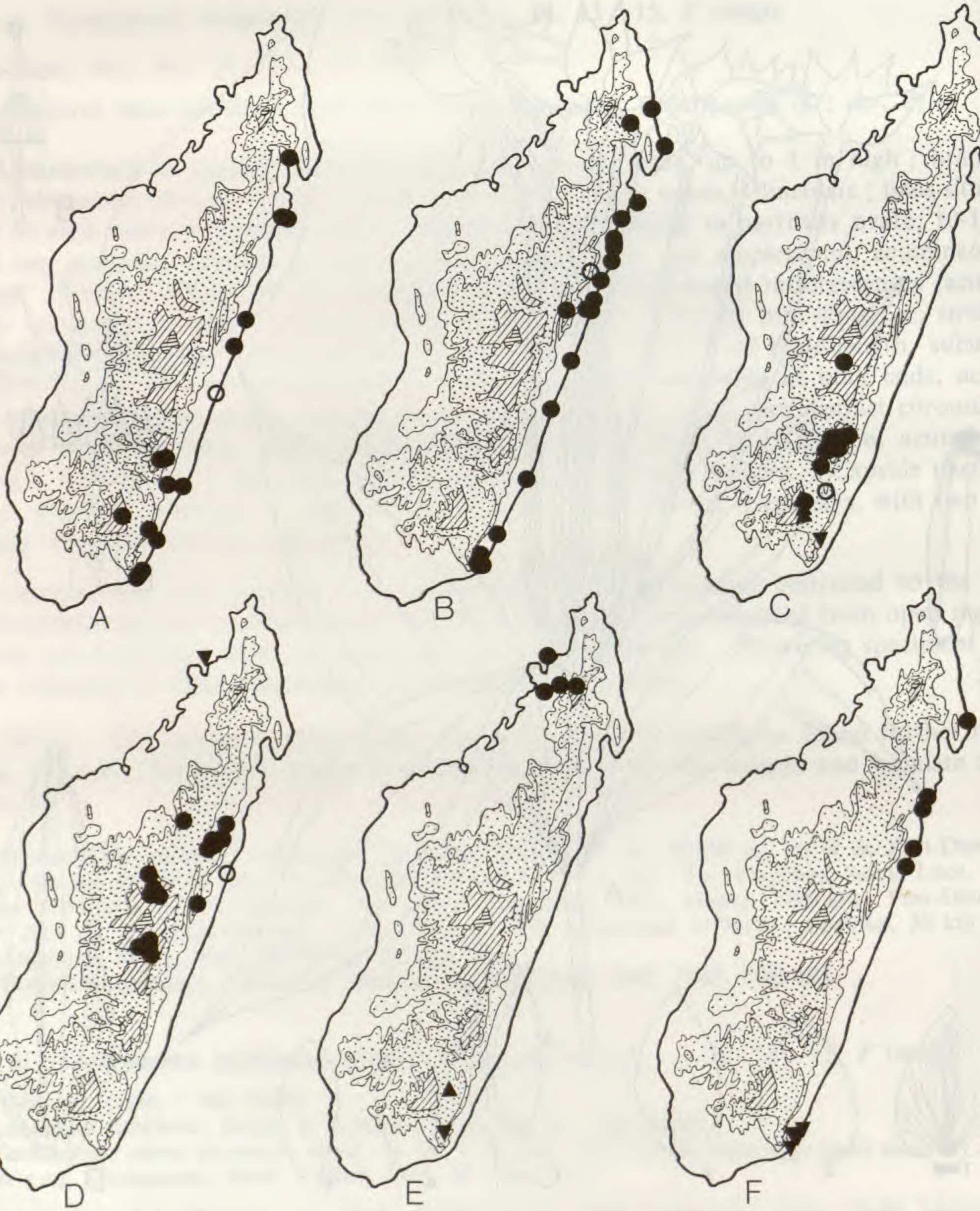
— *Tachiadenus elatus* HEMSLEY, Hook. Ic. Pl. 6 (3), *tab. 2554* (1898). Lectotype (here selected) : *Curtis s.n.*, Madagascar, *Herb. ?Hitch 1897*, (K ; iso-, P).

TYPE : *du Petit-Thouars s.n., Herb. Willdenow no. 3563, Lisianthus*, (holo-, B-W, photograph seen).

Probably sparsely to moderately branched shrublet, up to 3 m high ; branches erecto-patent ; internodes shorter than leaves. Stem terete, without lines. Leaves narrowly elliptic to narrowly ovate to usually ovate, 10-18 × 4-7 cm, gradually tapering at base with



Pl. 14. — **Tachiadenus tubiflorus** : **A**, habit ×0.5 ; **B**, dissected upper part of flower (B′ = configuration of the stamens within the tube) × 1.5 ; **C**, calyx whole and dissected × 1.5 ; **D**, flower in fruit with corolla and most of calyx removed × 1.5 ; **E**, anther × 6. (A, *s. coll., Herb. Jard. Bot. Tananarive 3328*, P ; B, C, E, *Capuron s.n.*, Tampolo, S ; D, *Perrier de la Bâthie 13257*, P).



Pl. 15. — **Distribution maps of Tachiadenus** (○ = approximate locality) : **A**, *T. gracilis* ; **B**, *T. carinatus* ; **C**, *T. vohimavensis* (▼), *T. platypterus* subsp. *platypterus* (●) and subsp. *angustialatus* (▲) ; **D**, *T. longiflorus* (●) and *T. pervillei* (▼) ; **E**, *T. boivinii* (●), *T. antaisaka* (▼) and *T. umbellatus* (▲) ; **F**, *T. longifolius* (▼) and *T. tubiflorus* (●).

long petiole, not amplexicaul, acute to acuminate, 3-nerved. Flowers rather many together in umbel-shaped inflorescences (actually condensed cymes) terminal at branches ; pedicels rather short, 5-10 mm long, straight. Calyx 12-18 mm long, asymmetric with two narrower outer and three broader inner lobes ; lobes coalescent 1/5 or less of their length, much overlapping at base ; outer lobes ± elliptic, tapering at both ends, acute at apex, 4-6 mm wide ; inner lobes ovate to broadly ovate, one or both sides truncate at base, acute at apex, 8-10 mm wide ; wings absent. Corolla white ; tube 9-16 cm long, with distinct coronula of callus at mouth of tube ; lobes ovate, 25-45 × 10-17 mm, acute to acuminate. Anthers 3-4 mm long, with large, large-celled appendix at apex and two smaller ones at bases of thecae. Capsule narrowly ovoid, 25-30 × 8-12 mm, much longer than calyx, with two protruding mid-walls entirely coriaceous.

DISTRIBUTION AND HABITAT : *T. tubiflorus* is restricted to the northern half of the eastern coast of Madagascar along the shore. It grows in humid sublittoral forests on sand. Flowering specimens seen from April, May and August to December.

NOTES : This species is unique in *Tachiadenus* in many characters. It has terete stems totally lacking lines or wings, broad flat unequal calyx lobes and conical anthers furnished with glands at the end of the connective and at the base of the thecae. Furthermore, it is the only species with large rounded seeds. It has a distinctly decussate somewhat elongated umbel-shaped inflorescence.

HEMSLEY (1898) cited collections of GERRARD, HUMBLOT, BARON and CURTIS under his *T. elatus*. I have chosen a sheet of CURTIS in Kew which is the base of the drawing accompanying the protologue.

SPECIMENS EXAMINED. — DIEGO-SUAREZ : Forêts sublittorales entre Ambalobe et Ambohitralanana, Antalaha, 1967, *Capuron 27756 SF* (P) ; Distr. Antalaha, Cant. Ambohitralanana, 1953, *Silazy 5442 RN* (P). — TAMATAVE : Tampolo au N de Fenerive, 1957, *Capuron s.n.* (K, P, S) ; Fenerive, forêt de Tampolo, *Debray 1871* (P) ; Fenerive Est, 1912, *Perrier 9033* (P) ; Tampina (Tampani) au S de Tamatave, 1920, *Perrier 13257* (K, P) ; R.N. 2, Canton Amlohitalanan, Distr. Antalaha, 1953, *Saboureau 5442 RN* (P) ; Tamatave, environs d'Ivoloina, 1937, *Herb. Jard. Bot. Tananarive 3328* (P) ; Soanierana-Ivongo, 1949, *Service Eaux Forêts Madagascar 2378* (P).

INEXACT OR UNIDENTIFIED LOCALITIES : North Madagascar, *Baron 6682* (K, P) ; Madagascar, *Chapelier 61* and *s.n.* (P, S) ; Madagascar, 1897, *Curtis s.n.* (K, P) ; Distr. de Fenerive, S de la rivière Azofo, 1909, *Geay 8939, 8955, 8957, 9059* (P) ; Madagascar, *Gerrard ?43* (K) ; *Humblot 7* (K, LD, P, S) ; *S. loc.*, 1920, *Perrier 13257* (P) ; Madagascar, *Herb. Drake s.n.* (P) ; Madagascar, *Herb. Richard s.n.* (P) ; *S. loc., Herb. du Petit-Thouars s.n.* (P).

EXCLUDED TAXA

Tachiadenus continentalis Baker (1895 : 70) = **Belmontia teuszii** Schinz. This species, though much resembling the genus in habit, is not a *Tachiadenus*. It has a short and bilocular ovary. It furthermore differs in the morphology of the calyx and by having longer filaments, an accentuated coronula at the filament bases and a large broad appendix at the anther apex.

Tachiadenus mechowianus (Vatke ex Schinz) Hill (1908 : 337) = not *Tachiadenus*. The type specimen (*Mechow 503* in Zurich) is not a *Tachiadenus*. It has a short and bilocular ovary as in *Exacum, Ornichia* and *Sebaea*, without nerves at the only shortly coales-

cent calyx lobes as in *Sebaea*, and the anthers are adhering to each other by large papillae along the margins as found in *Ornichia*.

Tachiadenus parviflorus Baker (1897 : 274) = **Cataranthus lanceus** (Bojer) Pichar.

Tachiadenus trinervis (Desr.) Griseb. (1839 : 201) = **Ornichia trinervis** (Desr.) Klack.

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